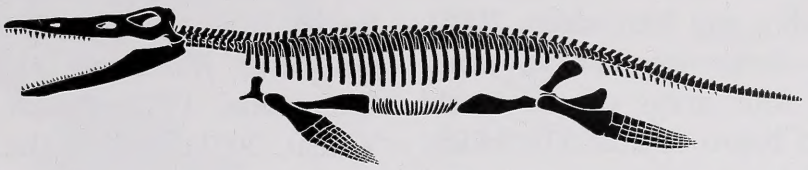
BREVIORA

Museum of Comparative Zoology



US ISSN 0006-9698

CAMBRIDGE, MASS. 8 MAY 2012 NUMBER 529

A NEW AMBER-EMBEDDED SPHAERODACTYL GECKO FROM HISPANIOLA, WITH COMMENTS ON MORPHOLOGICAL SYNAPOMORPHIES OF THE SPHAERODACTYLIDAE

JUAN D. DAZA[1] AND AARON M. BAUER[1,2]

ABSTRACT. A new species of *Sphaerodactylus* (Squamata: Gekkota: Sphaerodactylidae) is described from an amber inclusion from the late Early Miocene or early Middle Miocene (15 to 20 million years ago) of the Dominican Republic. Unlike earlier amber-embedded specimens assigned to this genus, the new specimen is largely skeletal, with some integument remaining. A combination of 258 (of 674) osteological and external characters could be scored for the new species in a cladistic analysis of 21 gekkotan species, including representatives of all sphaerodactylid genera.

The most parsimonious trees obtained confirm the placement of the amber gecko within the genus *Sphaerodactylus* and a comparison with extant Hispaniolan and Puerto Rican congeners suggests phenetic similarity both with members of *S. difficilis* complex and the *S. shrevei* species group. Character mapping on the basis of the phylogenetic analysis permits the preliminary identification of morphological characters diagnostic of the Sphaerodactylidae, Sphaerodactylini, and *Sphaerodactylus*. Osteological features of the new species are discussed in the broader context of sphaerodactyl, sphaerodactylid, and gekkotan variation. Extant Hispaniolan *Sphaerodactylus* display significant ecomorphological variation and it is likely that the many known, though not yet described, amber-embedded specimens will eventually reveal similar patterns in their Miocene congeners.

KEY WORDS: *Sphaerodactylus*; Sphaerodactylidae; gecko; osteology; Hispaniola; new species; phylogeny

INTRODUCTION

Amber-embedded fossils provide unique insights into extinct vertebrate taxa as they frequently preserve the integument and thus give an impression of what the intact animal looked like in life. The mode of amber preservation, however, limits vertebrate inclusions to taxa small enough to be trapped in the viscous resin. Thus, aside from isolated bird feathers (e.g., Grimaldi and Case, 1995; Alonso *et al.*, 2000; Perrichot *et al.*, 2008) and mammal hairs and bones (MacPhee and Grimaldi, 1996;

[1] Department of Biology, Villanova University, 800 Lancaster Avenue, Villanova, Pennsylvania 19085, U.S.A.; e-mail: juan.daza@villanova.edu, aaron.bauer@villanova.edu.

[2] Department of Herpetology, Museum of Comparative Zoology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, U.S.A.

© The President and Fellows of Harvard College 2012.

SHOUT
SHARE
IT

Sontag, 2008), known vertebrate inclusions are limited to several minute frogs (Poinar and Cannatella, 1987; Poinar, 1992; Grimaldi, 1996), unidentified (but probably squamate) skin pieces (Poinar and Poinar, 1999; Grimaldi *et al.*, 2002; Perrichot and Néraudeau, 2005), and to a fairly large number of small lizards. At least four areas of the world have yielded such lizard fossils. The oldest inclusion is *Baabdasaurus xenurus*, an autarchoglossan of indeterminate affinities described from a partial specimen in amber from the Lower Cretaceous (120 million years ago [MYA]) of Lebanon (Arnold *et al.*, 2002). A 100-million-year-old gekkotan in amber, *Cretaceogekko burmae*, is known from deposits in Myanmar (Arnold and Poinar, 2008). Amber deposits of the Baltic, dating from the early Eocene (Larsson, 1978; Ritzkowski, 1997; Weitschat and Wichard, 2002), have yielded a minimum of three different species in the extinct lacertid genus *Succinilacerta* (Katinas, 1983; Kosmowska-Ceranowicz *et al.*, 1997*a*, 1997*b*; Krumbiegel, 1998; Böhme & Weitschat, 1998, 2002; Borsuk-Białynicka *et al.*, 1999) and a single gekkotan, *Yantarogekko balticus* (Bauer *et al.*, 2005).

The greatest number of amber lizards, however, are known from the Miocene of the Dominican Republic. These fossils include several specimens referred to the dactyloid genus *Anolis* (Lazell, 1965; Rieppel, 1980; de Queiroz *et al.*, 1998; Polcyn *et al.*, 2002), and several geckos referable to the extant genus *Sphaerodactylus* (Böhme, 1984; Kluge, 1995). Although a very limited number of lizards in Dominican amber have been formally described, many more specimens are known to exist in the holdings of private collectors (Poinar and Poinar, 1999; D. A. Grimaldi, personal communication).

Biostratigraphic and paleogeographic data indicate that the amberiferous deposits in the Dominican Republic were formed in a single sedimentary basin during the late Early Miocene through early Middle Miocene, about 15 to 20 MYA (Grimaldi, 1995; Iturralde-Vinent and MacPhee, 1996). Amber fossils from tropical America originate mainly from the resin of the extinct leguminous tree *Hymenaea protera* (Poinar and Cannatella, 1987; Poinar, 1992; Iturralde-Vinent, 2001), and on the basis of inference from historical forest distribution in Hispaniola, these trees were mainly distributed in the evergreen forests of the southeast area, surrounding the depositional basin (Iturralde-Vinent and MacPhee, 1996). Today, Dominican amber is commercially exploited in three geological formations: La Toca (North), Yanigua (Eastern), and Sombrerito (south of the Cordillera Central in the area of Plateau Central–San Juan).

We here report on a new amber-embedded gecko from La Toca mine, in the Cordillera Septentrional, Santiago Province, north of Municipio Santiago de los Caballeros (Fig. 1). We further review osteological data for the Sphaerodactylidae and identify putative synapomorphies that support the monophyly of this recently recognized clade of gekkotans. To date only two nonmolecular characters, neither found in all members of the clade, have been identified as possible evidence of affinities:

1. presence of parafrontal bones (present in *Aristelliger* and *Teratoscincus* and presumably lost in all miniaturized sphaerodactylids) and

2. single-egg clutch (except in *Teratoscincus* and *Euleptes,* which retain two-egg clutches; Gamble *et al.*, 2008a).

MATERIALS AND METHODS

Anatomical Observations. Faked lizard inclusions in amber are common, so the authenticity of the specimen was confirmed on the basis of several criteria intrinsic to both

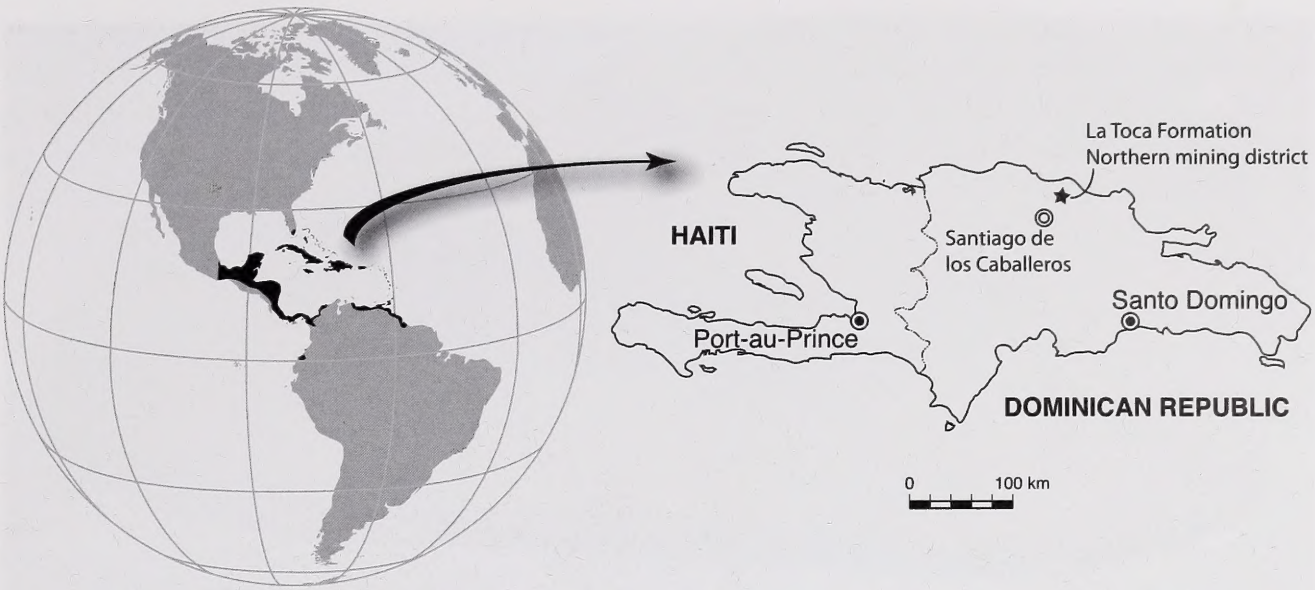


Figure 1. Left, black areas indicate the distribution of *Sphaerodactylus* geckos in the Americas. Right, map of Hispaniola showing the type locality of *Sphaerodactylus ciguapa* sp. nov. (modified from Iturralde-Vinent, 2001).

the amber itself and the lizard it contained (Bauer and Branch, 1995). The amber specimen and comparative ethanol-preserved, cleared and stained, and dry skeletal material were examined using a Nikon SMZ1000 dissecting microscope equiped with a digital camera (Nikon DS-Fi1) and the image acquisition software NIS Elements D v. 3.1, and a Leica MZ6 dissecting microscope equipped with a camera lucida. Digital radiographs were obtained using a Kevex™ PXS10-16W X-ray source and Varian Amorphous Silicon Digital X-Ray Detector PaxScan® 4030R set to 130 kV at 81 µA. For each X-ray linear and pseudofilm filters were used. Drawings were traced directly over digital images using Adobe® Illustrator® CS3 13.0.2 and complemented with illustrations made with the camera lucida. Measurements were made from the X-ray images to avoid measurement error caused by the refractive index of amber (n = 1.55). Anatomical terminology follows Daza *et al.* (2008).

Phylogenetic Analysis. To objectively identify characters uniting the new species with its congeners and other members of the Sphaerodactylidae, a cladistic analysis of selected taxa was performed. A morphological data set of 674 characters scored for 21 taxa (Appendix 1; data available at www.morphobank.org; project number p532, accession number X1201) was analyzed in the computer program T.N.T. (Goloboff *et al.*, 2003a, 2008) using maximum parsimony. All characters were treated as unordered, and equally weighted. In addition to representatives of 12 sphaerodactylid genera, including all six genera of "sphaerodactyls," seven outgroup gekkotan species were included: *Hemidactylus brookii*, *Narudasia festiva*, and *Pseudogekko smaragdinus* (Gekkonidae), and *Phyllodactylus wirshingi*, *Gymnodactylus geckoides*, *Thecadactylus rapicauda*, and *Tarentola mauritanica* (Phyllodactylidae). Our sampling outside sphaerodactylids is minimal considering the diversity of the Gekkota as a whole and we recognize that taxon sampling may significantly affect tree topology. However, as our focus is on the characters that define Sphaerodactylidae, sphaerodactyls, and *Sphaerodactylus* we believe that this limitation will not materially affect our results. Twenty independent searches were done using defaults of "xmult" plus 10 cycles of tree drifting (Goloboff, 1999). Support was estimated

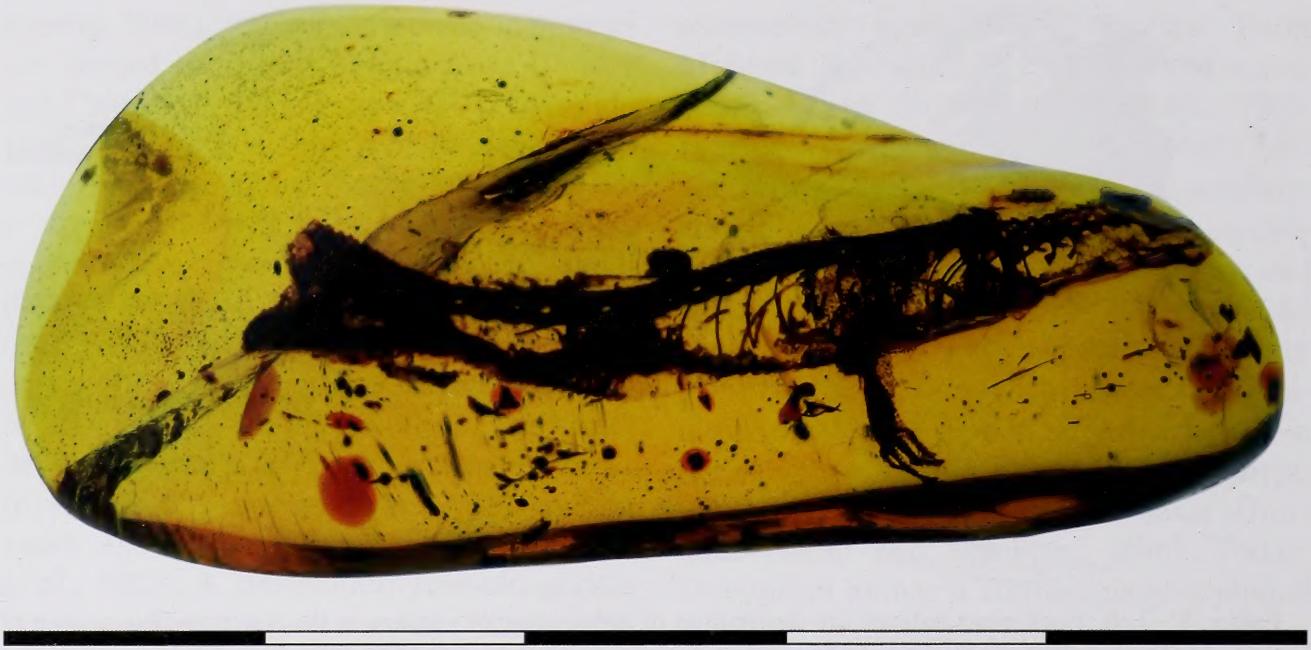


Figure 2. Right lateral view of *Sphaerodactylus ciguapa* sp. nov. Scale bar = 5 cm.

through Bremer support indices (BS; Bremer, 1994), relative Bremer support indices (relative fit difference [RFD]; Goloboff and Farris, 2001), bootstraps, and symmetric resampling (SR) expressed as GC values (difference in frequencies for groups supported–contradicted; Goloboff *et al.*, 2003b).

External and osteological features of additional taxa of *Sphaerodactylus* and other sphaerodactylids (Appendix 2) were also compared in the course of diagnosing the new species, but were not incorporated into the phylogenetic analysis. Original descriptions and other references (Schwartz and Graham, 1980; Schwartz and Thomas, 1983; Schwartz and Henderson, 1991) were consulted for further information about body size and scalation features of *Sphaerodactylus* spp.

Institutional Abbreviations. Material examined was obtained from the following collections: Aaron M. Bauer personal collection, Villanova University, Villanova; (AMB); American Museum of Natural History, New York (AMNH); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FMNH); James Ford Bell Museum, University of Minnesota, Saint Paul (JFBM); Museum of Comparative Zoology, Harvard University, Cambridge (MCZ); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ), Museu de Zoologia, Universidade de São Paulo, São Paulo (MZUSP); Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, Norman (OMNH); Richard Thomas personal collection, Universidad de Puerto Rico, Rio Piedras, Puerto Rico (RT); Museo de Zoología, Universidad de Puerto Rico, Rio Piedras (UPRRP); United States National Museum, Washington (USNM; USNMFH—Field Series); Colección de Herpetología de la Universidad del Valle, Cali, Colombia (UV-C).

Description of new species *Sphaerodactylus ciguapa* Daza and Bauer, new species

Figures 2–7

Holotype. MCZR-186380, amber-embedded, nearly complete skeleton with patches of integument. Collected from the late Early Miocene to early Middle Miocene (15 to

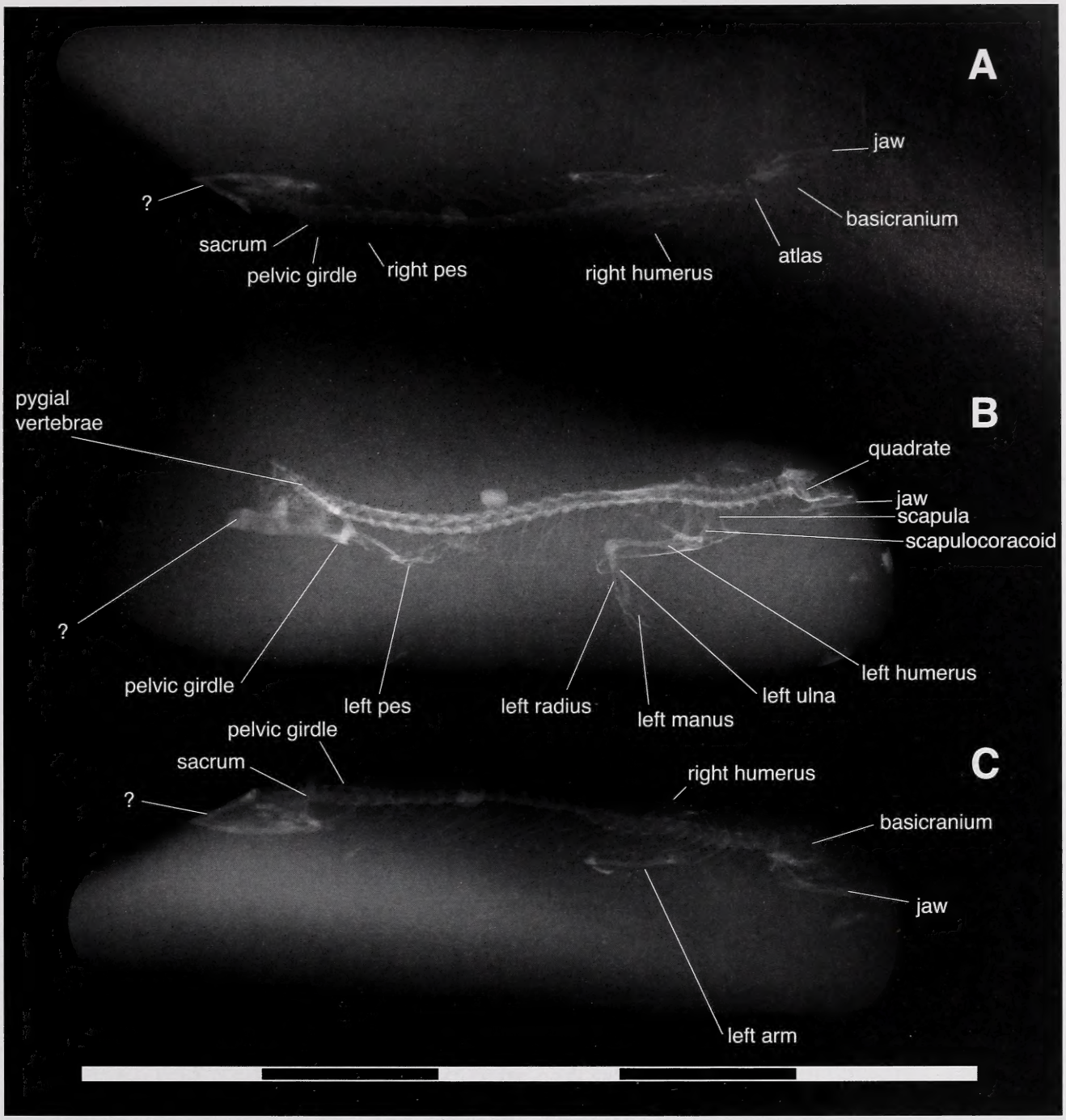


Figure 3. (A) Dorsal, (B) lateral, and (C) ventral X-rays of *Sphaerodactylus ciguapa* sp. nov. Scale bar = 5 cm. The partially radiopaque "V"-shaped element in the caudal area labeled with a question mark may represent a portion of the regenerated tail or an artifact unrelated to the specimen itself.

20 MYA) amber deposits of La Toca mine, in the Cordillera Septentrional, Santiago Province, north of Municipio Santiago de los Caballeros, Dominican Republic.

Diagnosis. A medium-sized *Sphaerodactylus* with an estimated snout–vent length (SVL) of 33 mm. Basicranium with narrow clinoid process; rounded crista alaris; straight crista prootica; squarish paroccipital process; knoblike sphenoccipital tubercle; fenestra ovalis completely visible in ventral view; foramen magnum roughly oval. Clavicles each with a single enlarged fenestra; interclavicle with broad lateral arms; 26

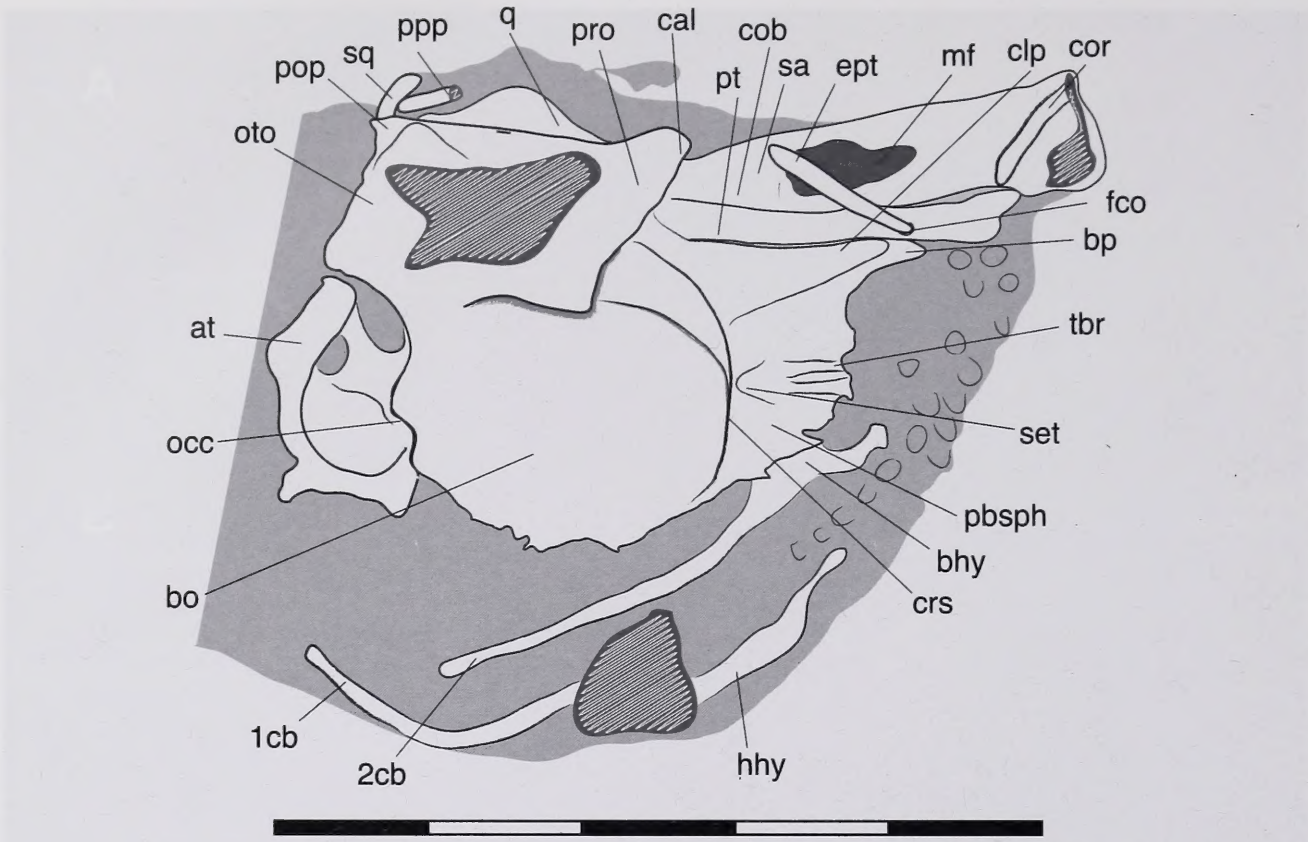


Figure 4. Dorsal view of basicranium, jaw, hyoid apparatus, and atlas of *Sphaerodactylus ciguapa* sp. nov. Gray areas with white zig-zags indicate portions of the specimen worn during polishing. Abbreviations: 1cb, first ceratobranchial; 2cb, second ceratobranchial; at, atlas; bhy, basihyal; bo, basioccipital; bp, basipterygoid process; cal, crista alaris; clp, clinoid process; cob, compound bone (angular, articular, prearticular); cor, coronoid; crs, crista sellae; ept, epipterygoid; fco, fossa columellae, hhy, hypohyal; mf, mandibular fossa; occ, occipital condyle; oto, otooccipital; pop, paroccipital process; ppp, postparietal process; pro, prootic; pt, pterygoid; q, quadrate; sa, surangular; set, sella turcica; pbsph, parabasisphenoid; sq, squamosal; tbr, trabeculae. Scale bar = 5 mm.

presacral vertebrae; pelvis with large and ventrally directed pectineal process; digits short, with manual metacarpals twice the length of the phalanges; fourth phalangeal element of the fourth manual digit short. Gular and body laterodorsal scales small, rounded posteriorly, and juxtaposed to weakly imbricate; some lateral scales distinctly keeled; forelimb scales smooth and strongly imbricate; claw enclosed by three scales.

Ninety-nine extant and one fossil species of *Sphaerodactylus* are currently recognized as valid (Böhme, 1984; Kluge, 2001; Uetz, 2011). In general, *Sphaerodactylus* are known as endemics of small areas (Schwartz and Henderson, 1991; Henderson and Powell, 2009); because of this it is reasonable to compare this fossil with the 35 extant species from Hispaniola, as well as the other fossil species. However, because the age of the Dominican amber deposits is older than, or contemporaneous with, estimations of the formation of the Mona Passage and the separation of Hispaniola and Puerto Rico (~16–11 MYA; Iturralde-Vinent and MacPhee, 1996; MacPhee *et al.*, 2003) we also compared the new species with 10 extant species from the "Puerto Rico Area" (*sensu* Thomas, 1999), an area that includes the islands of Mona, Monito, and Desecheo as well as Greater Puerto Rico (*sensu* Thomas and Schwartz, 1966) (Appendix 2; species endemic to St. Croix, U.S. Virgin Islands were not included as

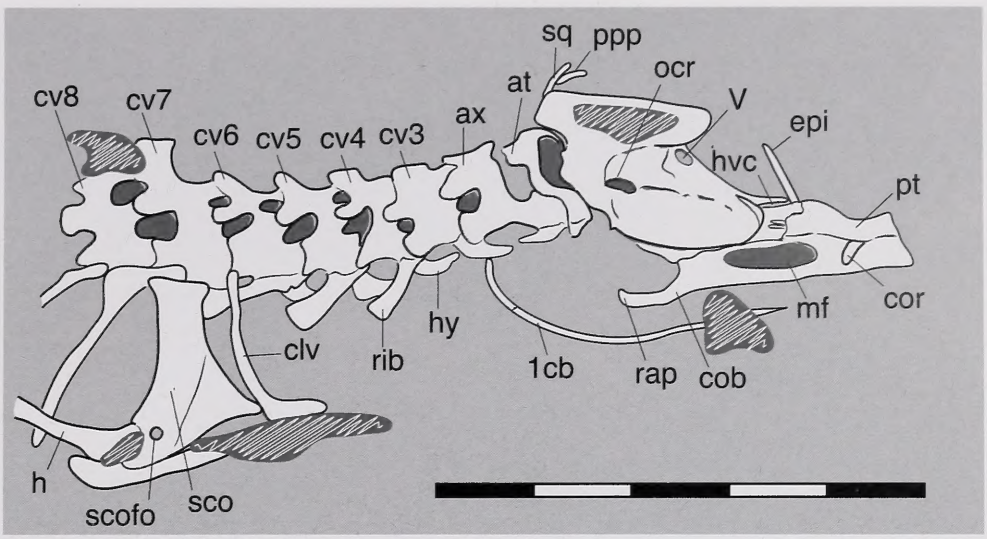


Figure 5. Right lateral view of *Sphaerodactylus ciguapa* sp. nov. showing skull, cervical vertebrae, and pectoral girdle. Gray areas with white zig-zags indicate portions of the specimen worn during polishing. Abbreviations: 1cb, first ceratobranchial; at, atlas; ax, axis; clv, clavicle; cob, compound bone; cor, coronoid; cv#, cervical vertebrae #; epi, epipterygoid; h, humerus; hvc, groove for the course of the lateral head vein; hy, hypapophyses; mf, mandibular fossa; ocr, occipital recess; ppp, postparietal process; pt, pterygoid; rap, retroarticular process; rib, rib; sco, scapulocoracoid; scofo, scapulocoracoid foramen; sq, squamosal; V, incisura prootica for the course of the trigeminal nerve. Scale bar = 5 mm.

this island is not part of the Puerto Rican Bank).

The specimen of *S. ciguapa* is skeletally mature (see Discussion), and is comparable in size (here we have considered 29–36-mm SVL to be in the same size range of *S. ciguapa*) to 17 extant species from Hispaniola (*S. altavelensis*, *S. armstrongi*, *S. asterulus*, *S. cinereus*, *S. clenchi*, *S. darlingtoni*, *S. difficilis*, *S. lazelli*, *S. leucaster*, *S. randi*, *S. rhabdotus*, *S. samanensis*, *S. savagei*, *S. schuberti*, *S. shrevei*, *S. thompsoni*, and *S. zygaena*), four from the Puerto Rico Area (*S. monensis*, *S. klauberi*, *S. macrolepis*, *S. micropithecus*), and to the amber-preserved species *S. dommeli* (Böhme, 1984). Of these 22 species, *S. ciguapa* may be distinguished from *S. monensis*, *S. macrolepis*, and *S. thompsoni* by its much smaller dorsal scales, from *S. samanensis* by its larger and more swollen scales, from *S. cinereus* by its heterogeneous dorsal scalation including imbricating, keeled scales (versus granular dorsal scalation), and from all others except *S. asterulus*, *S. difficilis*, *S. dommeli*, *S. rhabdotus*, and *S. shrevei* by its swollen, weakly keeled to keelless dorsal scales (versus flat scales with strongly to very strongly keeled scales, see Fig. 8 for examples of scale features discussed). The new species may be distinguished from *S. rhabdotus* by its more weakly keeled and subimbricate (versus strongly keeled and strongly imbricate) dorsal scales, and from *S. asterulus*, *S. difficilis*, and *S. shrevei* by the presence of an extremely large clavicular fenestra (versus a small fenestra). The amber-embedded *S. dommeli*, which comes from the same mine area as *S. ciguapa*, may be differentiated on the basis of its smaller, more granular dorsal scales (see Böhme, 1984, fig. 3). Additionally, we were unable to identify enlarged clavicular fenestrae in X-rays of *S. dommeli*.

General Description. The fossil is enclosed in an oval piece of polished amber measuring 48.5 mm in its maximum dimension. The specimen lies close to one of the margins of

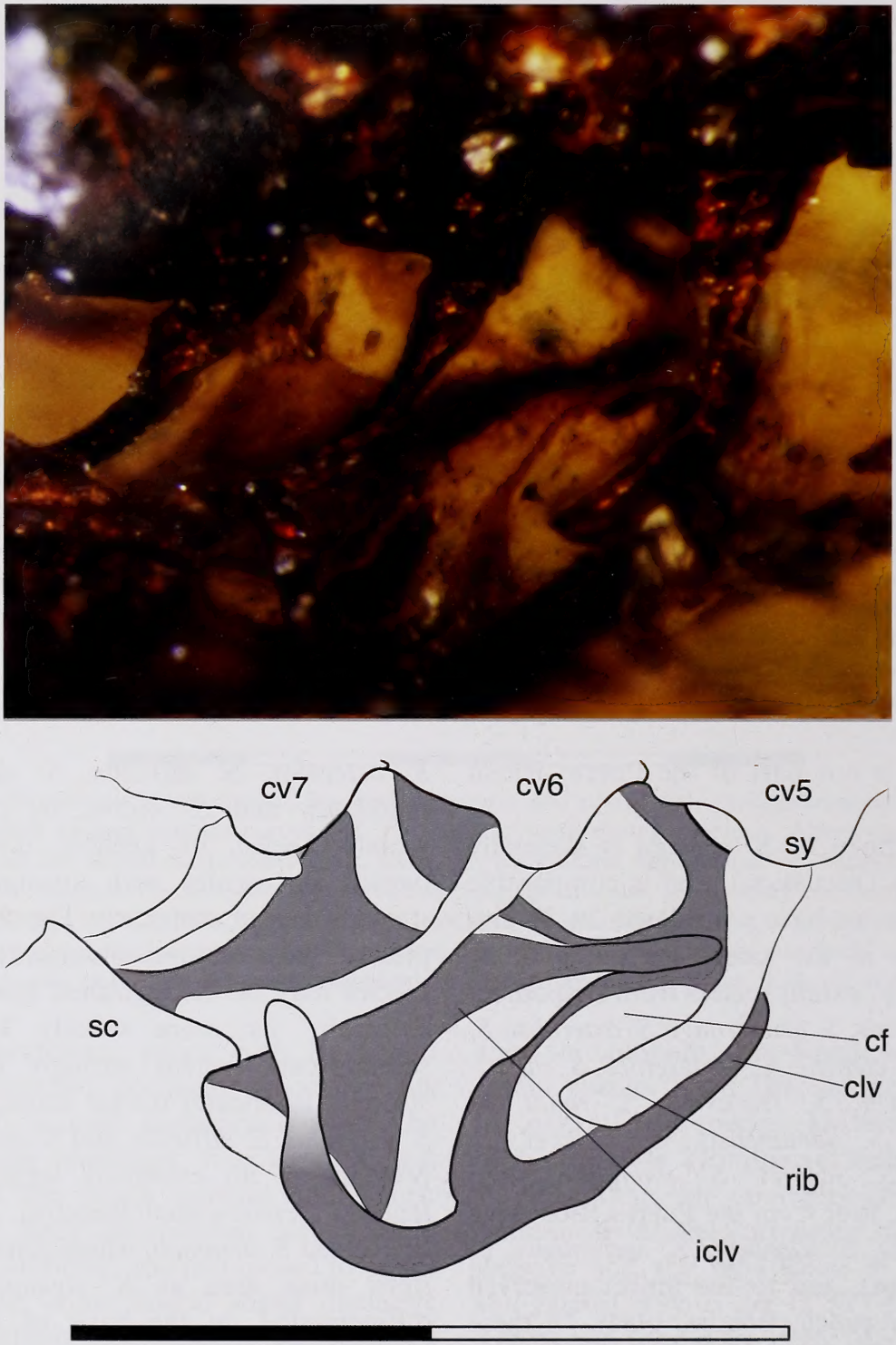


Figure 6. *Sphaerodactylus ciguapa* sp. nov. in dorsolateral view showing portions of the pectoral girdle. Scale bar = 2 mm.

the piece and in some spots it is exposed as a result of the polishing process. The amber has a partial fracture plane at the posterior end of the specimen, but the two portions remain together. The amber matrix embedding the specimen is semitransparent yellow and the bone color is dark brown, providing a contrast that facilitates observation of the whole specimen (Fig. 2). The specimen is mainly skeletonized (Figs. 2, 3), with a few

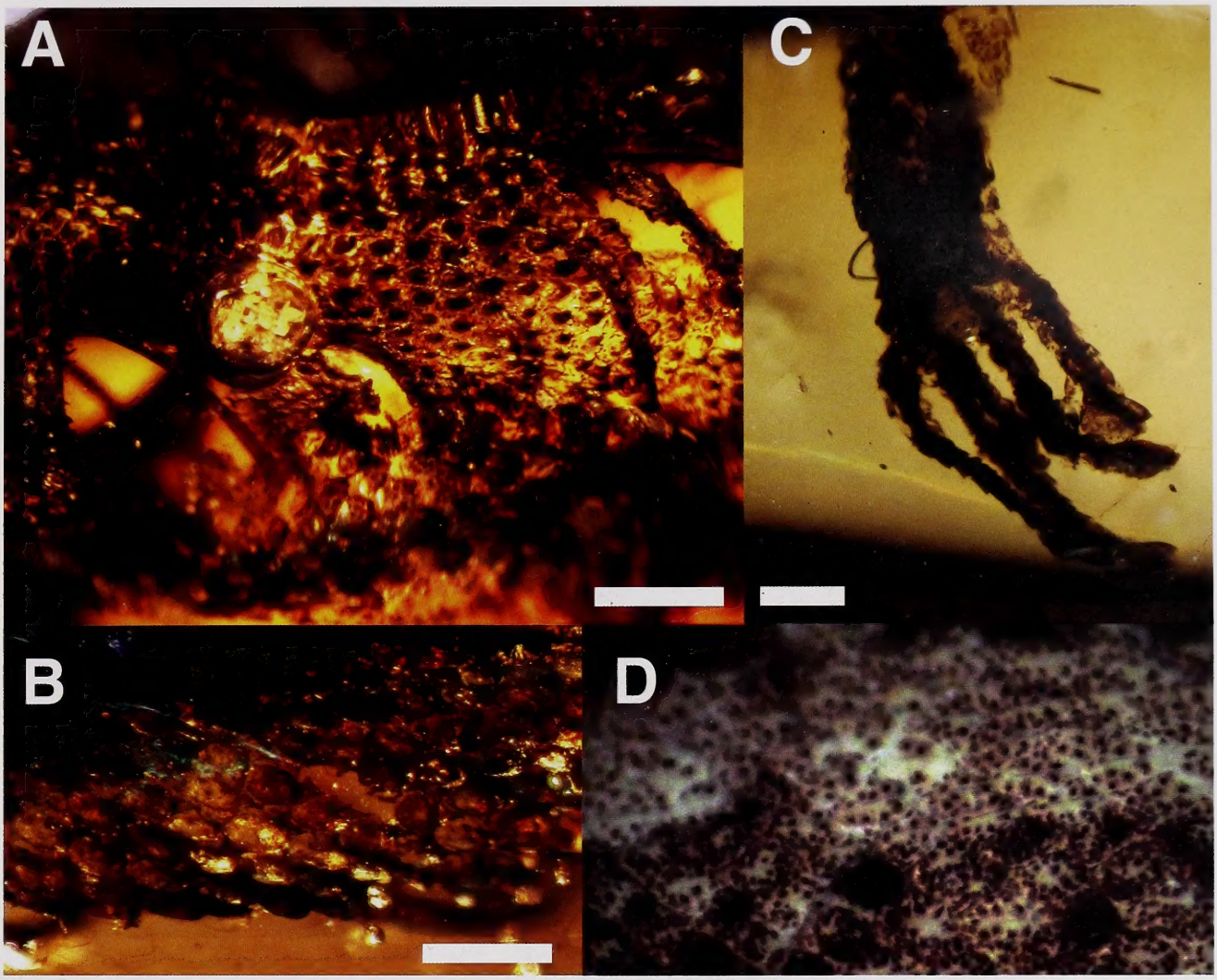


Figure 7. *Sphaerodactylus ciguapa* sp. nov. showing (A) left laterodorsal scapular integument, (B) mid-trunk dorsal scales adjacent to the vertebral line, (C) left hand showing the typical *Sphaerodactylus* scalation pattern around the claw, and (D) dorsal scales of *S. difficilis* (USNM 328965), an extant species from Hispaniola with similar scalation to *S. ciguapa*. Scale bar = 0.5 mm.

scattered patches of skin. The skeleton preserves the posterior half of the left pterygoid, a portion of the left epipterygoid, a tiny fragment of the left parietal, left squamosal, left quadrate, and some portions of the brain case (including left prootic, left otooccipital, parabasisphenoid, and basioccipital), the posterior part of the right mandibular ramus, parts of the hyoid apparatus, all of the cervical, thoracolumbar, sacral, pygal, and some postpygal caudal vertebrae, the left arm and the proximal portion of the right humerus, both suprascapulas, scapulocoracoids, and clavicles, the complete sternum, the pelvis, left femur and tibia, and both feet. All elements, except the right pes, are articulated.

Holotype Measurements (unless otherwise stated, measurements were made along the long axis of each element; for paired elements, left side measurement is provided): braincase from the tip of the basipterygoid process to the occipital condyle: 3.66 mm; quadrate length from the cephalic condyle to the mandibular condyles: 1.9 mm; squamosal: 0.71 mm; jaw fragment: 3.28 mm; cervical + thoracolumbar vertebrae: 24.91 mm; sacrum length: 0.88 mm; sacrum width: 2.31 mm; tail

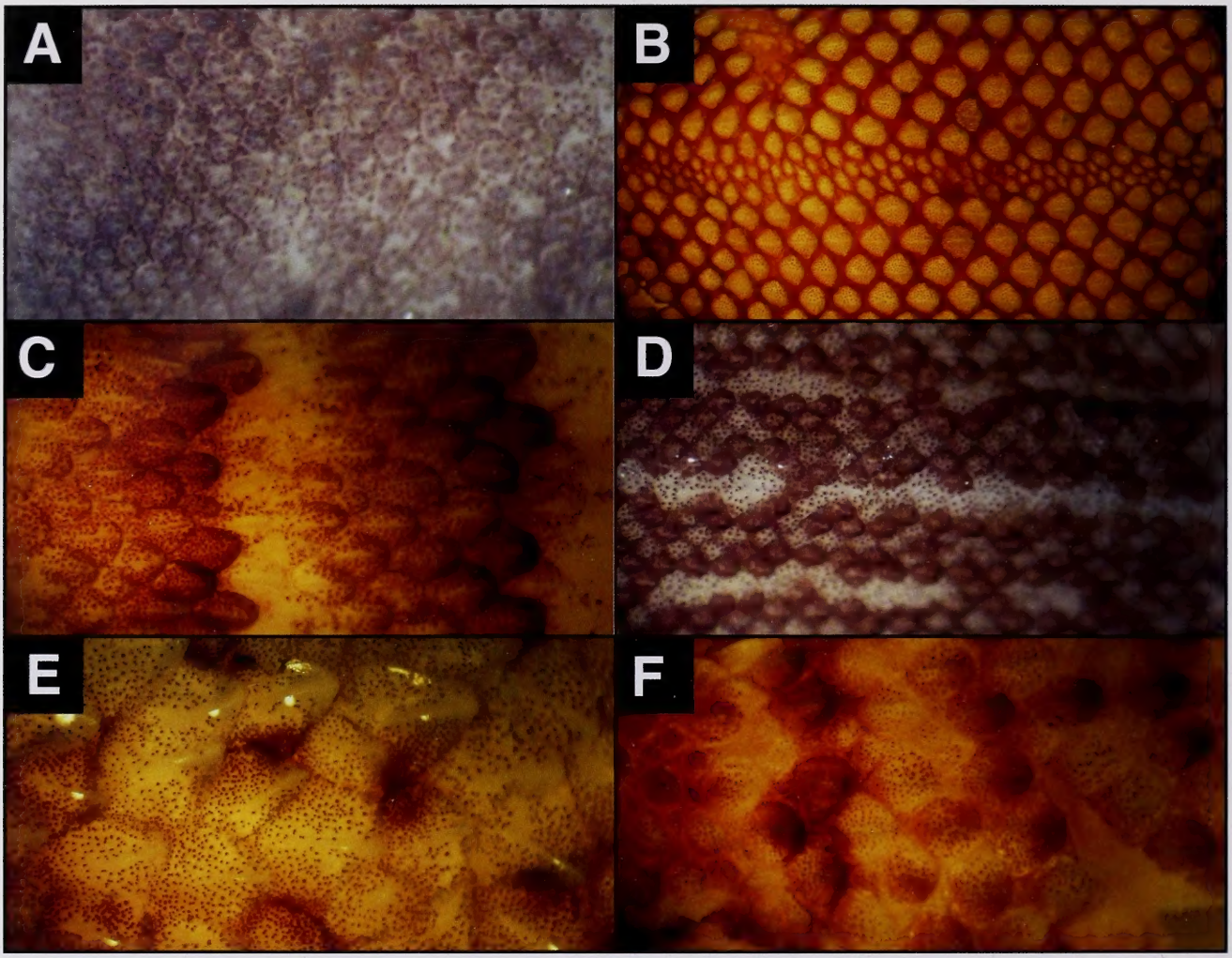


Figure 8. Dorsal scale variation in *Sphaerodactylus* geckos. (A) *S. pacificus* (USNM 157531, small, rounded, swollen, juxtaposed), (B) *S. rosaurae* (USNM 570205, medium, rounded, swollen, juxtaposed, with a middorsal zone of granular scales), (C) *S. parkeri* (USNM 328281, large, rounded, not swollen, imbricate), (D) *S. argus* (USNM 251978, small, acute, not swollen, imbricated), (E) *S. richardsoni* (USNM 252126, large, acute, swollen, imbricate), (F) *S. thompsoni* (USNM 328977, large, rounded, swollen, juxtaposed).

(proximal segment only preserved): 3.77 mm; scapulocoracoid from the fossa glenoidea to the dorsal margin: 2.28 mm; humerus: 4.46 mm; ulna: 3.23 mm; radius: 2.79 mm; third manual digit + metacarpal: 2.43 mm; pelvic girdle from the epipubic cartilage to the posterior edge of illium: 3.31 mm; metischial process: 0.35 mm; tibia: 2.77 mm; third pedal digit + metatarsal: 3.31 mm.

Dermatocranium. The parietal is only represented by the tip of the posterior end of the left postparietal process (ppp, Figs. 4, 5); the postparietal process is very narrow and contacts the squamosal laterally at the midpoint of this bone, as in other sphaerodactyls. The squamosal (sq, Figs. 4, 5) is small, slightly curved, and rounded in cross-section. Its distal end contacts the braincase and the top of the quadrate. A fragment of the left pterygoid (pt, Figs. 4, 5) extends from a point anterior to the fossa columellae (fco, Fig. 4) to the end of the quadrate process. Basispterygoid–pterygoid, epipterygoid–pterygoid, quadrate–pterygoid, and craniomandibular skull joints are preserved. The former two are synovial and the latter a syndesmosis (Frazzetta, 1962; Payne *et al.*, 2011). In lateral view the pterygoid is mostly

straight; it possesses a large facet for the basipterygoid joint that is visible in medial view.

Splanchnocranium. A nearly complete left epipterygoid (ept, Figs. 4, 5) is preserved, although the dorsal portion of this bone is broken and is disarticulated from the prootic. Only the left quadrate bone (q, Figs. 3, 4) is preserved. The bone is completely convex and the dorsal margin is rounded with no lateral indentation. Although the craniomandibular joint is *in situ*, it can be seen that the distal articular surface bears two condyles, and that the lateral is slightly larger than the medial one. The presence and position of the quadrate foramen cannot be established in the specimen. The left auditory meatus is nearly intact, and includes portions of the tympanic membrane, implying that the left stapes is preserved within the middle ear, although it is not visible.

Neurocranium. The parabasisphenoid complex (pbsph, Fig. 4) is fused posteriorly to the basiocciptal. The left basipterygoid process (bp, Fig. 4) is short but expanded distally and anterolaterally oriented. It is partially covered by a long, narrow clinoid process (clp, Fig. 4) that roofs the notch on the basipterygoid process and marks the course of the lateral head vein (hvc, Fig. 5). The right basipterygoid process is missing. The paired trabeculae (tbr, Fig. 4) are clearly distinguishable; they are round in cross-section and parallel to one another. Posterior to the trabeculae, the sella turcica (set, Fig. 4) is bounded posteriorly by an anteriorly curved crista sellae (crs, Fig. 4). The anterior opening of the Vidian canal is located ventral to the crista sellae. Most of the basioccipital (bo, Fig. 4) is preserved; it is concave dorsally and forms part of the double occipital condyle (occ, Fig. 4) and the ventral border of the foramen magnum. The sphenoccipital tubercle epiphysis is small and knoblike and is located anteriorly, causing the crista tuberalis to be inclined posterodorsally. The left prootic (pro, Fig. 4) is preserved but its medial surface is partly worn down because of the polishing process. The crista alaris is rounded and small, and does not overhang the inferior process of the prootic. The inferior process bears the incisura prootica, which in geckos is closed, forming an oval foramen that surrounds a portion the mandibular branch of the trigeminal nerve, CN5 (V, Fig. 5). A portion of the left otooccipital (oto, Fig. 4) is present, but none of the foramina in the occiput (i.e., vagus and hypoglossal foramina) are discernable.

Mandible (Figs. 3–5). The posterior portion of the left jaw comprises the posterior process of the coronoid (cor), the surangular (sa), compound bone (cob; angular, prearticular and articular), and, on the labial side, the posterior portion of the dentary. A wide mandibular fossa is formed by the surangular and the compound bone. This fossa opens laterally through a small slit (external mandibular fenestrae) that marks the separation between the partially fused surangular and the compound bone (Daza *et al.*, 2008).

Hyoid Apparatus (Figs. 4, 5). A portion of the basihyal (without the glossohyal process) is preserved. The second epibranchials are articulated to the basihyal and oriented almost parallel to one another, as in *S. macrolepis* (Noble, 1921). Both first epibranchials are preserved and curve upward toward the posterior portion of the braincase. Anterior to the right second ceratobranchial there is an elongated bony structure that could be a portion of the right hypohyal.

Vertebral Column. All the presacral vertebrae are preserved. The total number is 26, as is typical for most geckos. There are eight cervical vertebrae (Fig. 5), which follows the commonest formula for lizards: 3 (ribless) + 3 (short distal widened ribs) + 2 (long slender

ribs) = 8 (Hoffstetter and Gasc, 1969). The intercentra of the atlas, axis, and third–sixth cervicals bear ventral hypapophyses and are positioned intervertebrally, remaining unfused from the vertebrae centra (type A, Hoffstetter and Gasc, 1969). The hypapophyses are double in the atlas and axis and single in the remaining cervicals. The orientation of the hypapophyses varies ventrally (atlas), posteriorly (axis), and anteriorly (remaining cervicals). The height of the seventh and eighth cervicals is 25% greater than that of the anterior cervicals, having taller and squarer neural arches when viewed laterally. These last two cervical vertebrae are more similar to the thoracolumbar series. All vertebrae bearing ribs have synapophyses (parapophysis + diapophysis; Hoffstetter and Gasc, 1969) that project laterally from the anteroventral part of the centrum (Fig. 5). The short ribs of cervical vertebrae 4–6 are not bifurcated distally (cv4–cv5, Fig. 5), but in sphaerodactyls, these ribs have a cartilaginous terminus that is not preserved in the fossil. Ribs from the fourth and fifth cervicals are free, and the sixth and seventh contact the medial surface of the scapulocoracoid. The dorsal process of the clavicle contacts the dorsal surface of the sixth vertebral rib. Four or five vertebrae are connected to the sternum via sternal ribs (Fig. 3). The remaining thoracic vertebrae have long ribs that decrease in length posteriorly, each bearing small postxiphisternal inscriptional ribs. There is one ribless lumbar vertebra. The sacrum has fused transverse processes; the first sacral has an expanded transverse process that overlaps the second sacral. The exact number of pygal vertebrae (i.e., caudals lacking chevrons; Russell, 1967; Hoffstetter and Gasc, 1969) could not be determined, but there are at least five caudal vertebrae with elongated transverse processes. The tail seems to be regenerated, appearing as a poorly defined cartilaginous rod that is broken and bent and is situated along the posterior portion of the body (?, Fig. 3).

Pectoral Girdle and Forelimbs (Fig. 6). The two clavicles are expanded medially, rotated forward, and articulated medially, contacting the anteroventral end of the interclavicle. The clavicles each have a single fenestra, which is among the largest seen in any sphaerodactyl examined.

Pelvic Girdle and Hind Limbs (Fig. 3). The pelvic girdle and hind limbs are mainly covered by integument and are only visible in the X-rays. The ischium, pubis, and ilium—which is articulated with the sacrum—are fused. The two inominate bones are still articulated at the pubic (epipubic cartilage preserved) and ischial symphyses, forming a large ischiopubic fenestra (Figs. 3A, C). The pectineal process of the pubis is large and ventrally directed, as in all sphaerodactyls (Noble, 1921; Gamble *et al.*, 2011a). The posterior flange of the ischium is more or less straight. The left acetabulofemoral joint is preserved; the left leg retains all of its elements. Of the right hind limb, only the pes, which is twisted and facing the front of the pelvis, is preserved. An exact phalangeal formula cannot be determined from the X-rays because of the superposition of the vertebrae, but all *Sphaerodactylus* known have manual and pedal formulae of 2:3:4:5:3 and 2:3:4:5:4, respectively, with phalanges 2 and 3 of digit 4 of both manus and pes shortened (Russell and Bauer, 2008).

Integument. There are scales present in the gular, dorsolateral trunk, and apendicular regions. Gular scales are small, flattened, rounded posteriorly, not swollen, and juxtaposed; lateral scales covering the scapular blade and the body flanks are small, moderately keeled, rounded to subacute posteriorly, slightly swollen, and juxtaposed with little or no imbrication (Fig. 7A); dorsal scales on the mid-trunk are slighty larger, unkeeled to

weakly keeled, oval, slightly swollen, and subimbricate to weakly imbricate (Fig. 7B). The scales covering the forelimbs are rounded posteriorly, smooth and strongly imbricated; the claw is enclosed by three scales, which are arranged in the typical asymmetrical pattern of *Sphaerodactylus* (Fig. 7C): an enlarged outer inferolateral, a terminal + median dorsal, and an inner inferolateral (*sensu* Parker, 1926), or ventral, dorsal, and ventrolateral (*sensu* Kluge, 1995).

Etymology. "La Ciguapa" is a Spanish name for a mythical humanoid of Dominican folklore. It is described as a woman with brown or dark blue skin, whose feet face backward, and who has a very long mane of smooth, glossy hair that covers her naked body (Angulo Guridi, 1866; Pérez, 1972; Ubiñas Renville, 2000, 2003). It is supposed to inhabit the high mountains of the Dominican Republic. The name, treated here as a noun in apposition, recalls the dark brown bones and twisted feet in the holotype specimen and the source of the specimen in the Cordillera Septentrional of the Dominican Republic. The Ciguapa legend has been proposed to be derived from the "opias" (spirits of the dead) of the indigenous Caribbean Taíno people (Bosch Gaviño, 1935).

RESULTS

Phylogenetic Analysis. Rooting with any of the outgroup taxa resulted in the same ingroup topology and measures of support, so *Hemidactylus brookii* was arbitrarily chosen to root all trees presented herein. Tree searches found four most parsimonious trees (MPT) of 1,135 steps (Consistency index [Ci] = 0.379. Retention index [Ri] = 0.404). Two of these trees recovered a monophyletic Sphaerodactylidae, as strongly supported by molecular data (Gamble *et al.*, 2008a, 2008b, 2011b); therefore we used one of these trees as working hypothesis for mapping characters. Nine internal nodes are well supported, with absolute BS values greater than or equal to 3, and relative BS values above 11. Five of these nine nodes also had bootstrap values above 82 and GC values above 77 (Fig. 9).

In the selected topology *Aristelliger lar* + *Teratoscincus scincus* are sister to remaining sphaerodactylids, with *Quedenfeldtia*, *Euleptes*, and *Saurodactylus* as sequential sister taxa to the clade formed by sphaerodactyls + *Pristurus*. Among the most parsimonious trees the positions of *Lepidoblepharis* and *Sphaerodactylus* are interchangeable within the sphaerodactyls.

Character Mapping. As previously noted, there are only two nonmolecular characters that currently serve to diagnose the family Sphaerodactylidae, and neither of these is expressed in all members of the group or is exclusive to the clade. Thus, the monophyly of this family has not yet been tested using morphological data. Here we present all the characters that apply to each of three nested clades on the basis of their mapping on the preferred most parsimonious tree. For each one of named clades we emphasize those characters that exhibit less homoplasy and may therefore be useful for the morphological diagnosis of these groups. Characters that could be scored on *S. ciguapa* are indicated in bold numbers.

Sphaerodactylidae: This clade inludes all the genera listed in Gamble *et al.* (2008a) and is supported by seven characters: 10) convex snout; 136) dagger-shaped anterolateral process of frontal; 308) anterior inferior alveolar foramen surrounded by dentary, splenial, and angular; 334) anterior tip of splenial narrow and pointed; 439) branched xiphisternum; **506)** metatarsal V greatly hooked (see Discussion); **560)** two pygial vertebrae. Of these characters, 506 was not present in any other sampled gekkotan, whereas char-

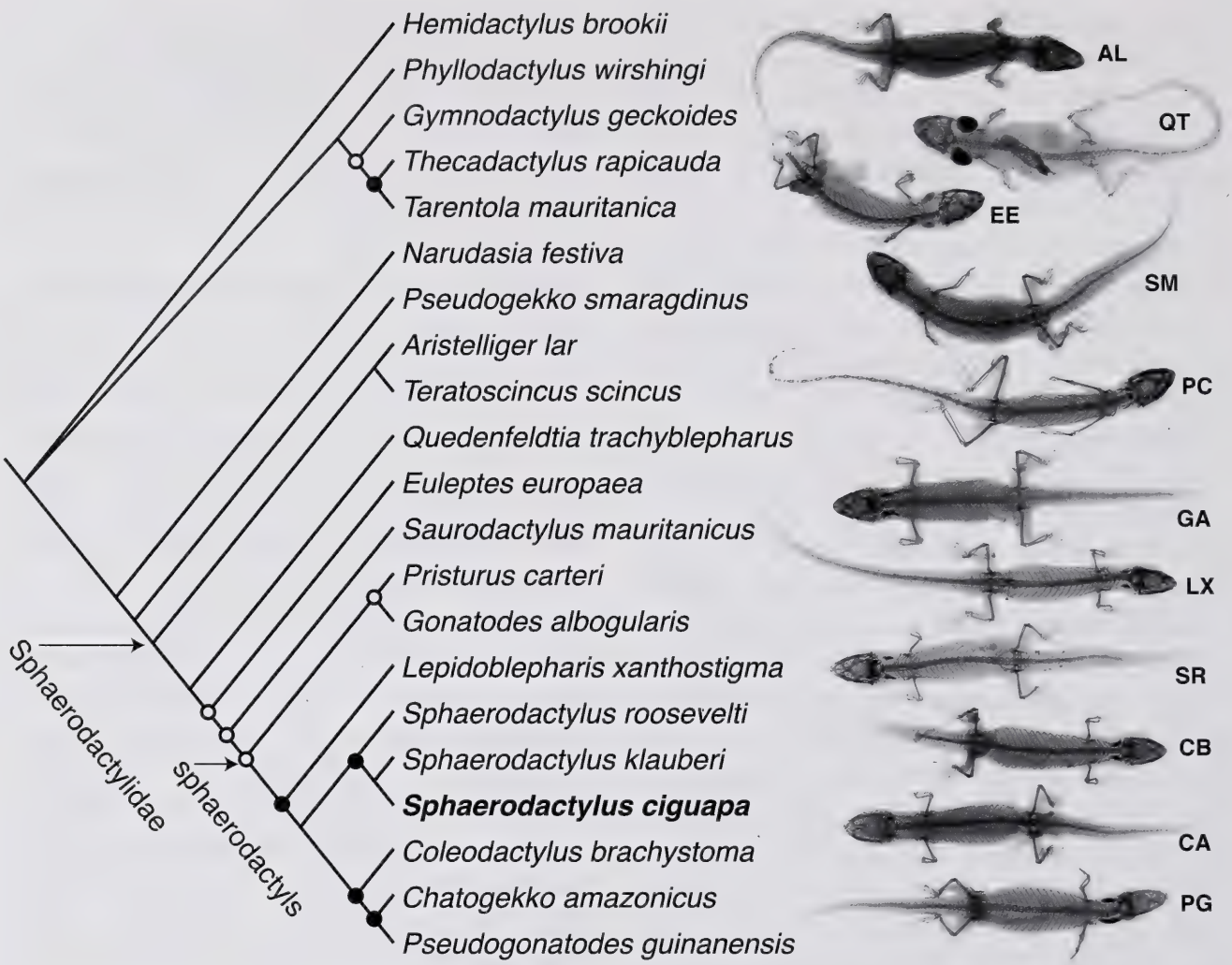


Figure 9. One of four most parsimonious trees of gekkonoid geckos. Circles at nodes denote BS/RFD equal to or higher than 3/11, filled circles further indicate boostrap/GC values higher than 82/78. X-rays of representative sphaerodactylid geckos from the tree are shown at right (not to same scale). Initials next to each X-ray correspond to the the genus and specific epithet of taxa represented on the tree.

acters 136 and 334, although present in all sphaerodactylids, are also found in some phyllodactylids.

Sphaerodactylini + *Pristurus*: This clade is supported by 11 characters: 19) fenestra vomeronasalis continuous within the fenestra exochoanalis; 37) ascending nasal process of the premaxilla separates nasals throughout approximately half their length; 93) postorbitofrontal large, with no reduction of processes; 97) postorbitofrontal ventrolaterally curved; 140) brief contact between the frontal and the maxilla; **266**) fusion of parabasisphenoid and basioccipital; 332) splenial fused to the coronoid; 352) surangular contacts dentary posterior to the coronoid–dentary suture; **440**) mesosternal extension absent; **454**) humeral ectepicondyle continuous, consolidated with the bone shaft; 601) nostril in contact with rostral scale. The least homoplasic character was 601, which is present only in *Aristelliger* outside sphaerodactyls. Although there were no exclusive characters for this clade, characters 93, 352, 440, and 454 were also invariably present among sphaerodactyls, but these character states occur in other sampled genera.

Sphaerodactyls: This clade is equivalent to Sphaerodactylini (Gamble *et al.*, 2008a). Althought this clade was not recovered in any of our MPTs, we performed a constrained search forcing this New World clade, which receives strong molecular support, to be monophyletic. We obtained a single MPT three steps longer than the shortest trees from the unconstrained analysis (1,138 steps; Ci = 0.353; Ri = 0.333). Eleven characters support this clade in the constrained analysis: 19) fenestra vomeronasalis continuous within the fenestra exochoanalis; 110) lacrimal foramen bounded by prefrontal and maxilla; 165) parietal nuchal fossa present and extending substantially onto the skull table; **184**) posterior end of squamosal not in contact with dorsum of quadrate; 201) secondary palate formed around choanal groove of palatine, ventromedial fold partly hides or hides most of the the choanal groove; 220) anterior point of the ectopterygoid relatively wide, abruptly tapering to point; **281**) crista prootica of prootic with straight margin (except in *Chatogekko*, which has a triangular crista prootica); 340) coronoid low, hardly elevated above jaw outline; **486**) pectineal process of pubis large and ventrally directed; 601) nostril in contact with rostral scale; 612) supraciliary spine present. Of these characters 201 and 340 were not present in any other sampled gekkotan. Other characters that show low homoplasy are 165 and 601 (also in *Aristelliger*), 184 (also in *Teratoscincus*), and 486 (also in *Thecadactylus*). Character 612 is also present in *Aristelliger* but lost in *Chatogekko*, *Coleodactylus*, and *Pseudogonatodes*.

Sphaerodactylus: Sixteen characters support this genus: 8) anterorbital portion of the skull equals 30% or less of the total skull length; 10) flat snout; 19) fenestra vomeronasalis and incisura jacobsoni separated; **28**) foramen magnum roughly oval; 98) postorbitofrontal, with large lateral process; **179**) postparietal process length less than half the length anterior to the parietal notch; 330) presence of angular and surangular processes of dentary; 347) the anterolingual process of the coronoid separates the dentary and splenial anteriorly; 368) 12–13 premaxillary teeth; **586**) body with keeled scales; 600) two to four loreal scales; 605) tympanic edge not smooth; **638**) digits with the distal-most superolateral scales in contact; 651) dorsal color pattern of head and nape with light stripes; 652) dorsal color pattern of body with ocelli; 671) ear partially occluded by flaps of skin. Of the characters listed, 330, 638, 651 were not found in any other sampled gekkotan. *Sphaerodactylus* geckos differ from other sphaerodactyls by characters 19 and 605. Other characters that were less homoplastic were 179 (also present in *Teratoscincus* and *Chatogekko*), 368 (also present in *Pseudogonatodes*), 586 and 600 (also present in *Chatogekko*), and 671 (also present in *Pristurus*).

DISCUSSION

Phylogeny. Four main hypotheses exist for the relationships of sphaerodactylid geckos (Fig. 10), two of them morphologically derived (Kluge, 1995; Arnold, 2009) and the others based on multigene analyses (Gamble *et al.*, 2008a, 2011b). There are discrepancies in the branching pattern between the morphological and molecular topologies, mainly with respect to the basal relationships within Sphaerodactylidae. Whereas the molecular phylogenies (Gamble *et al.*, 2008a, 2011b; Figs. 10C, D) include a clade comprising *Pristurus*, *Euleptes*, *Teratoscinus*, *Aristelliger*, and *Quedenfeldtia*, in the morphological hypotheses *Pristurus* was found to be either the sister taxon of all sphaerodactyls (Kluge, 1995; Daza, 2008) or *Pristurus* + *Quedenfeldtia* were sister to sphaerodactyls (Arnold, 2009). The sister group relationship between *Aristelliger* and *Quedenfeldtia* as suggested by

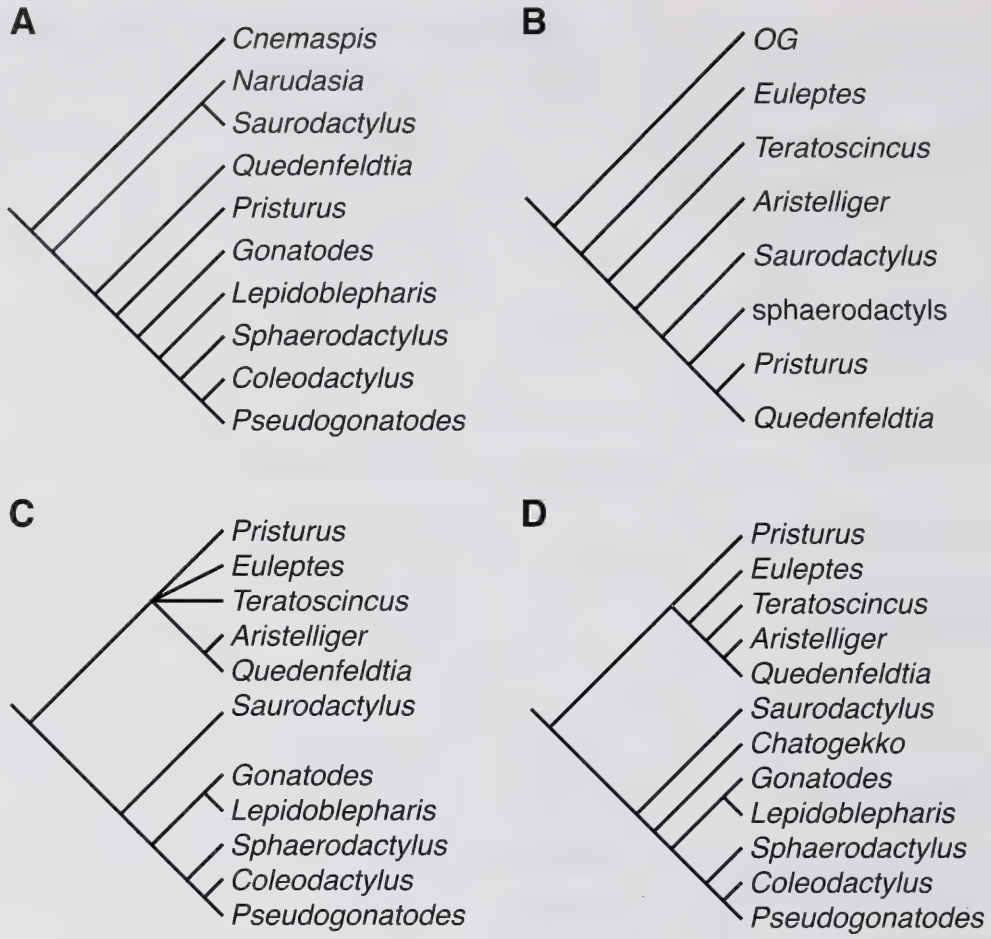


Figure 10. Phylogenetic relationships of sphaerodactylid geckos on the basis of previously published analyses. (A) Reanalysis of Kluge's (1995) morphological data set, (B) Arnold (2009), (C) Gamble *et al.* (2008a), and (D) Gamble *et al.* (2011b). "Sphaerodactyls" in Figure 10B includes all the miniaturized New World sphaerodactylids (i.e., *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, *Pseudogonatodes*, *Sphaerodactylus*, and the newly recognized *Chatogekko*).

multigene phylogenies is not congruent with our morphological results, in which an *Aristelliger* + *Teratoscinus* clade is supported by 14 morphological characters, one of them being the parafrontal bones, which are unique osteological structures in the circumorbital series only known in these two genera (Bauer and Russell, 1989; Daza and Bauer, 2010). The two molecular hypotheses differ mainly in the degree of resolution outside Sphaerodactylinae and in the placement of the extremely modified *Coleodactylus amazonicus* group (Figs. 10C–D), which has recently been recognized as a new sphaerodactyl genus, *Chatogekko* (Gamble *et al.*, 2011a).

The branching pattern we obtained for the sphaerodactyl clade is consistent with a previous morphological hypothesis (Kluge, 1995; Fig. 10A), but there is also a degree of taxonomic congruence between our hypothesis and recent multigene phylogenies (Gamble *et al.*, 2008a, 2011b). For instance, both molecular and morphological data provide strong support for the Sphaerodactylinae (i.e., sphaerodactyls + *Saurodactylus*), although they differ in the position of *Pristurus*.

Previous morphological analyses have not indentified synapomorphies that support Sphaerodactylidae; for instance, a reanalysis of Kluge's (1995) data set using the gekkonid genus *Cnemaspis* to root the tree results in a MPT in which *Narudasia* (another gekkonid) is nested within Sphaerodactylidae (Fig. 10A). Our new analysis including a superior number

of characters (approximately 27 and 55 times the number of morphological characters of Kluge [1995] and Arnold [2009], respectively) provides provisional empirical morphological evidence for the monophyly of Sphaerodactylidae and two clades nested within it. Although characters or combinations of characters support the monophyly of less inclusive clades like *Sphaerodactylus* and sphaerodactyls, relatively homoplasy-free characters supporting the Sphaerodactylidae remain elusive. The reduction of clutch size from two to one (see Gamble *et al.*, 2008a) remains a possible synapomorphy for the family, although on the basis of our topology (Fig. 9) it is equivocal if this character applies at the level of the Sphaerodactylidae as a whole, or to this clade exclusive of *Teratoscincus* + *Aristelliger*.

A strongly hooked metatarsal V was the least homoplastic trait supporting the Sphaerodactylidae in our analysis. Although this was not seen in any of the outgroup taxa in our phylogenetic analysis, this character is not exclusive to the Sphaerodactylidae, as both straight (Figs. 11A–C) and hooked (e.g., *Ailuronyx seychellensis*, Fig. 11D) morphologies occur in other gekkonoids. Among the Sphaerodactylidae this bone is variable but is always bent, being strongly hooked in some genera (e.g., *Aristelliger*, *Quedenfeldtia*, *Teratoscincus*; Figs. 11E–G) or more gently curved (e.g., sphaerodactyls, Fig. 11H).

Despite the fragmentary nature of *S. ciguapa* it was possible to score it for 258 characters (38.2% of the complete list). The analysis of these data unambiguously supports its placement within the genus *Sphaerodactylus*. Unfortunately in our phylogenetic analysis *Sphaerodactylus* was represented by only a few species from the *argus* series from Puerto Rico; hence this hypothesis is not useful for establishing the intrageneric relationships of *S. ciguapa*. Our comparisons with living taxa from Hispaniola and Greater Puerto Rico (see Diagnosis) suggest at least phenetic similarity with *S. difficilis*, a member of a widespread and diverse species complex (Thomas and Schwartz, 1983) in the *notatus* species group of the *argus* series, and with members (*S. shrevei*, *S. asterulus*, *S. rhabdotus*) of the *shrevei* species group (Schwartz and Graham, 1980) in the *cinereus* series. However, as these two groups span most of the phylogenetic diversity within West Indian *Sphaerodactylus* (Hass, 1991, 1996), the more specific affinities of *S. ciguapa* remain uncertain.

Morphology. The skeletal anatomy of at least some representative *Sphaerodactylus* geckos has been studied in detail (Noble, 1921; Parker, 1926; Daza *et al.*, 2008). In conjunction with the new data derived from *S. ciguapa* it is possible to reevaluate certain aspects of the osteology of the genus, and sphaerodactyls more broadly, within the more inclusive framework of the Gekkota.

The clinoid process of the parabasisphenoid is variable. In this fossil it is narrower than that described in *S. roosevelti* (Daza *et al.*, 2008), or observed in *S. difficilis*; it is unknown how variable this structure is across *Sphaerodactylus* species, but it might be a diagnostic character at some level. The paired (unfused) trabeculae in *Sphaerodactylus* are connected by a bony lamina in adults, including the type of *S. ciguapa*, whereas in juveniles these are discrete (Daza *et al.*, 2008). The sphenoccipital tubercle is reduced in small sphaerodactyls (excluding *Gonatodes*) and a similar reduction is present in miniaturized lizards from all gekkotan families (e.g., *Aprasia* [Pygopodidae], *Coleonyx* [Eublepharidae], *Narudasia* [Gekkonidae], *Homonota* [Phyllodactylidae]). The reduction of the apophysis that caps the sphenoccipital tubercle suggests modifications to the tendinous attachment of the fourth division of the *m. longissimus capitis*, which extends back into the ventral neck region along the fourth cervical in lepidosaurs (Al Hassawi, 2007)

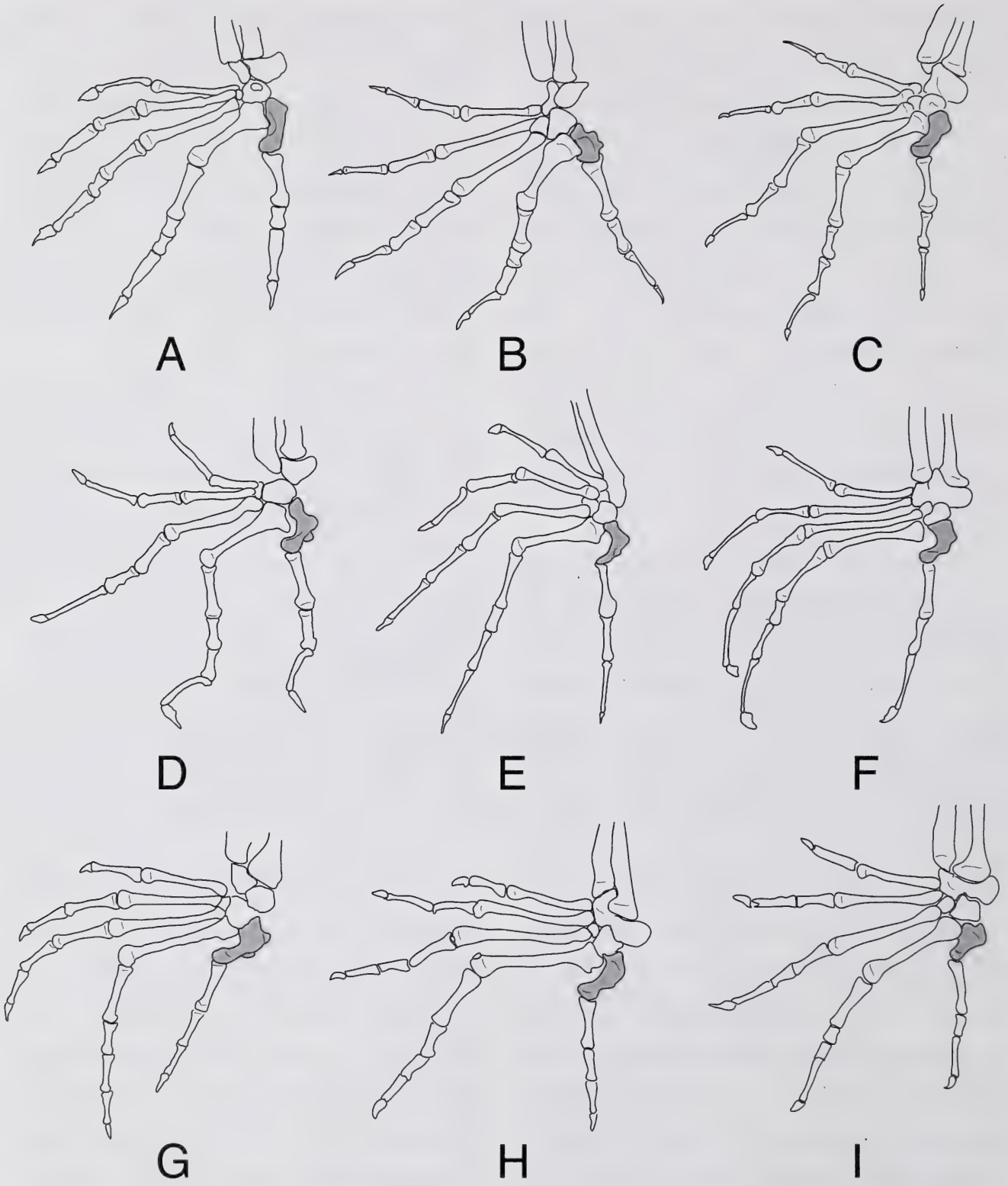


Figure 11. Left pes of some gekkonoid lizards showing variation on the shape of metatarsal V (shaded in gray) in phyllodactylids (A, B), gekkonids (C, D), and sphaerodactylids (E–I). (A) *Phyllodactylus wirshingi* (CAS 175498), (B) *Tarentola mauritanica* (UC MVZ 178184), (C) *Pseudogekko brevipes* (CAS 128978), (D) *Ailuronyx seychellensis* (CAS 8421, (E) *Aristelliger lar* (USNM 260003), (F) *Quedenfeldtia trachyblepharus* (USNM 196417), (G) *Teratoscincus scincus* (CAS 101437), (H) *Lepidoblepharis xantostigma* (USNM 313791), and (I) *Sphaerodactylus klauberi* (UPRRP 006416).

and whose fibers are attached to the ventral hypapophyses of the cervical vertebrae. Since reduction of this tubercle seems to be present only in small species, it is possible this is a character linked to miniaturization and might be related to a reduction of the neck muscle fibers.

In *S. ciguapa*, as in the rest of sphaerodactyls, the basicranial elements are fused, obscuring the sutures between the braincase bones. Observations of juveniles and newly hatched *Sphaerodactylus* indicate that the fenestra ovalis is bounded anteriorly by the prootic and posteriorly by the otooccipital (Daza *et al.*, 2008); hence this fenestra serves to estimate the limit between these two elements. In gekkotans the otooccipital has a synchondrosis articulation with the quadrate (Payne *et al.*, 2011), although this joint also has been described as syndesmosis (Webb, 1951). In geckos the articulation of the quadrate has been described as "paroccipital abutting" where this bone forms a well-defined articular process, which is applied against the anteroventral aspect of the paroccipital process (Rieppel, 1984). The paroccipital process of geckos has been described as thick or thin (Jollie, 1960), and this variation seems to be related to skull size, being generally elongated in larger species and reduced in small species. Similar variation has been seen in size series of amphisbaenians (Montero and Gans, 2008). *Sphaerodactylus* spp. have a small, thick paroccipital process that in posterior view is square (i.e., width and height subequal). Shape and size of the paroccipital process define its participation in the quadrate suspension in gekkotans. In *Pristurus*, *Gonatodes*, and *Lepidoblepharis* this process forms a true paroccipital abuttment, but in *Sphaerodactylus*, *Chatogekko*, *Coleodactylus*, and *Pseudogonatodes*, the quadrate is suspended from the lateral surface of the braincase, in front of the paroccipital process (pop, Fig. 4), with no participation of the squamosal. In very small forms (e.g., *Chatogekko*) the paroccipital process is so small that it has minimal or no participation in the suspension of the quadrate (Gamble *et al.*, 2011a).

Ventral to the paroccipital process is located the rounded occipital recess, which in adult lizards represents the recessus scale tympani (Oelrich, 1956; Rieppel, 1985) and which in *Sphaerodactylus* is exclusively surrounded by the otooccipital (Daza *et al.*, 2008). In other gekkonomorphs participation of the basioccipital in the margin of the occipital recess has been reported (Kluge, 1962; Grismer, 1988; Conrad and Norell, 2006). This participation is due to an outgrowth of the sphenooccipital tubercle; therefore the medial margin of the occipital recess is a good indication of the boundary between the otooccipital and the basiooccipital in forms with a fused braincase.

The perforated stapes, commonly present among sphaerodactylids, is uncommon among squamates; this feature has only been reported in some gekkotans, some amphisbaenians, and dibamids (Greer, 1976; Kluge, 1983; Rieppel, 1984; Gauthier *et al.*, 1988, Bauer, 1990; Conrad, 2008; McDowell, 2008). The only sphaerodactylid where the stapes is unperforated is *Saurodactylus*, where this bone is short and has a thick shaft and large footplate (Evans, 2008). Although in *S. ciguapa* this bone is not visible, it is very likely that it has a stapedial foramen like its congeners.

The number of presacral vertebrae among sphaerodactylids is variable; most of the genera have the most common gekkotan number of 26 (Hoffstetter and Gasc, 1969), whereas in *Quedenfeldtia* and *Pristurus* this number is reduced to 24 and 23, respectively. Arnold (2009) related the reduction of vertebrae in *Pristurus* species to a shift from active foragers to ambush predators. He also scored a reduction of presacral vertebrae in *Saurodactylus mauritanicus*, which was not corroborat-

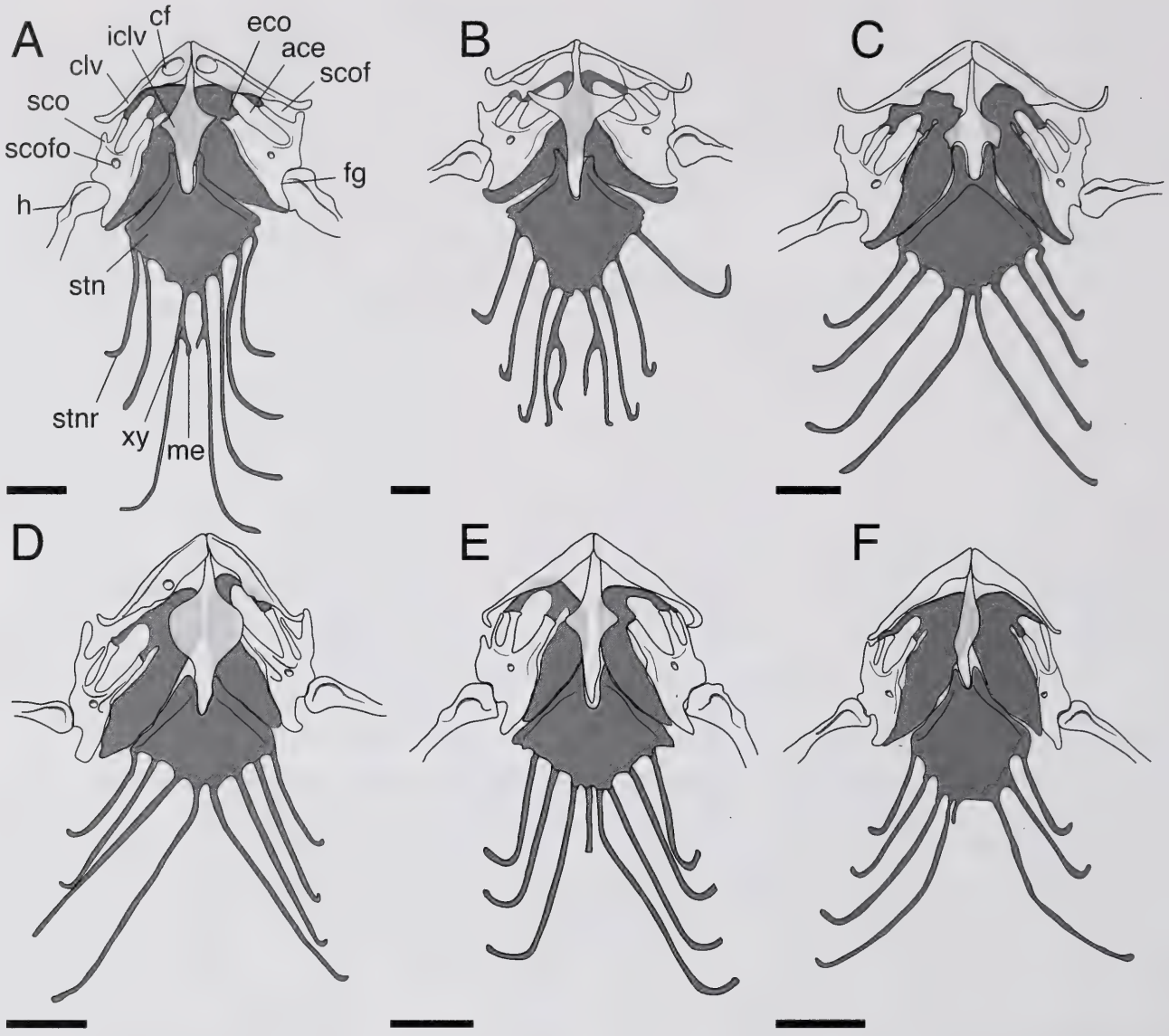


Figure 12. Ventral view of the pectoral girdles of sphaerodactyl geckos. (A) *Sphaerodactylus glaucus* (MVZ Herps 149093), (B) *Gonatodes albogularis* (MVZ Herps 83369), (C) *Lepidoblepharis xantostigma* (USNM 313791), (D) *Coleodactylus brachystoma* (MZUSP uncatalogued), (D) *Chatogekko amazonicus* (AMNH R 132039), (E) *Pseudogonatodes guinanensis* (MZUSP 94826). Abbreviations: ace, anterior coracoid emargination; cf, clavicular fenestra; clv, clavicle; eco, epicoracoid; fg, fossa glenoidea; h, humerus; iclv, interclavicle; me, mesosternal extension; sco, scapulocoracoid; scof, scapulocoracoid fenestra; scofo, scapulocoracoid foramen; stn, sternum; stnr, sternal rib; xy, xiphisternum. Scale bar = 1 mm.

ed by the specimens we reviewed. Reduction of presacral vertebrae explains the development of stocky bodies in *Quedenfeltia* and *Pristurus*, a process that according to the current morphological hypothesis and the molecular topologies would have been independently acquired (but see Arnold, 2009).

Centrum morphology of presacral vertebrae is procoelic in most sphaerodactyls, whereas *Gonatodes* has amphicoelous vertebrae (Hoffstetter and Gasc, 1969; Kluge, 1967, 1995). The formation of procoelous vertebrae in *Sphaerodactylus* proceeds differently from that in the rest of squamates. In these geckos the intervertebral tissue does not form a condyle but persists (Werner, 1971), suggesting that the procoelous vertebrae in these geckos might be derived from

amphicoelous ancestors (Hoffstetter and Gasc, 1969; Werner, 1971) with vertebrae resembling those of *Gonatodes*. Caudal vertebrae in sphaerodactyls have the first autotomy plane within the sixth or seventh caudal, as is consistent with *S. ciguapa*. It appears as if the type may have rebroken its tail at the proximal-most autotomy plane in an effort to escape when trapped in the resin.

A clavicular fenestra seems to be a constant character for *Sphaerodactylus* (Noble, 1921; Gamble *et al.*, 2011a), and this opening is huge in *S. ciguapa*. In *Gonatodes*, *Lepidoblepharis*, and *Chatogekko* the clavicles are unperforated (Figs. 12B, C, E; Noble, 1921; Parker, 1926; Gamble *et al.*, 2011a), whereas in *Coleodactylus* and *Pseudogonatodes* these may be closed or open, and the presence of a fenestra may be asymmetrical (e.g., Fig. 12D). The lateral arms of the interclavicle are another variable feature within sphaerodactyls (Kluge, 1995). In some *Sphaerodactylus*, including *S. ciguapa*, and in *Chatogekko* the arms are almost indistinguishable, producing an almost rhomboid interclavicle (Figs. 6, 12A, E); in *Gonatodes* the interclavicle is cruciform with elongated arms (Fig. 12B; Rivero-Blanco, 1976, 1979); *Lepidoblepharis* have short, squarish arms (Fig. 12C); *Coleodactylus* has broad, rounded arms (Fig. 12D); and in *Pseudogonatodes* interclavicle shape is variable—*P. barbouri* has an interclavicle with rounded lateral arms (Noble, 1921; Parker, 1926), and in *P. guinanensis* the interclavicles have no lateral arms (Fig. 12F). Variation in the development of the lateral arms of the interclavicle is likely to be correlated with differences in the posterior insertion of the sternohyoid muscle.

Although the appendicular skeleton presents no obviously phylogenetically informative characters, the epiphyses of the long bones are fused to the diaphyses, confirming that the type of *S. ciguapa* is skeletally mature.

Unfortunately scale descriptors have not been used consistently by different authors and variation, both between individuals and across the dorsum of single animals, can be extreme, rendering both the characterization and comparison of scalation difficult at best. Dorsal scale shape in *Sphaerodactylus* spp. varies from granular to elongate and strongly keeled (Fig. 8). When the scales are elongate they are typically extremely flattened and imbricate (Barbour, 1921). Although granular scales are common in related genera, truly granular scales covering the body dorsum are rarely present in *Sphaerodactylus* (Thomas, 1975). Among the only exceptions are *S. scapularis* from Gorgona Island in Colombia (Harris, 1982; J.D.D., personal observation) and Hispaniolan species such as *S. cinereus*, *S. elasmorhynchus*, and the extinct *S. dommeli*. *Sphaerodactylus copei*, another Hispaniolan species, has very large, swollen dorsals with a region of middorsal granular scales. The scalation of *S. ciguapa* may have been similar to this, but the fragmentary nature of the integument in the type makes it difficult to determine the actual distribution of scale types across the body and precise meristic comparisons with other congeners are precluded.

Ecology. Amber inclusions have revealed a good deal about the floral and faunal composition of the Miocene biota of the Dominican Republic (Poinar and Poinar, 1994, 1999). To the extent that available fossils permit the reconstruction of herpetofaunal communities of the period, they appear to be similar to those predominating today. Species of *Anolis*, *Sphaerodactylus*, *Typhlops*, and *Eleutherodactylus*, the four genera recorded as Dominican inclusions, today comprise 171 of 243 species of amphibians and reptiles found on Hispaniola (Hedges, 2011). Extant *Anolis* lizards are known for their distinctive ecomorphs and

have served as the basis for fruitful research programs in both ecology and evolution (Williams, 1976; Losos *et al.*, 1998; Losos, 2009). Hispaniolan *Sphaerodactylus* likewise seem to reflect morphological adaptation to particular lifestyles and substrates. Thomas (1975) and Thomas *et al.* (1992) proposed that head shape and coloration might be adaptive traits, an argument supported by replicated evolution of dark brown cryptic colored species in the montane species dwelling in the leaf litter from the Greater Antilles (Schwartz and Garrido, 1985). The study of this variation has the potential to provide a rich system for the study of comparative biology (D. Scantlebury, personal communication).

To date the only specimens of amber-preserved *Sphaerodactylus* that have been reported are *S. ciguapa*, two specimens of *S. dommeli* (Böhme, 1984), and an undescribed small (14 mm SVL + 16.6 mm tail length) specimen with slightly imbricated dorsal scales (Kluge, 1995). Kluge concluded that the last of these was possibly a juvenile on the basis of its small size, but *S. ariasae*, the smallest *Sphaerodactylus*, has an adult SVL range of 14.1–17.9 mm (Hedges and Thomas, 2001), so the possibility exists that this animal represents a very different ecomorph from the larger *S. ciguapa* and *S. dommeli*.

Although it may never be possible to fully reconstruct the *Sphaerodactylus* fauna of the Miocene, the study of the relatively large number of as yet undescribed amber geckos from the Dominican Republic (Poinar and Poinar 1999; D. A. Grimaldi, personal communication) may result in the description of additional new taxa and provide a clearer picture of the paleodiversity of this important group of Caribbean geckos.

ACKNOWLEDGMENTS

We thank James Hanken, Director of the Museum of Comparative Zoology, for purchasing the specimen described herein and making it available for our study. Yale Goldman provided locality data for the specimen and David Grimaldi (AMNH) provided advice on Dominican amber. Kyle Luckenbill and Ned Gilmore (Academy of Natural Sciences in Philadelphia) and Sandra Rareron and Kenneth Tighe (National Museum of Natural History, Smithsonian Institution) kindly helped with the X-rays. For access to comparative material we thank Richard Thomas (RT, UPRRP), Colin McCarthy (BMNH), Kevin de Queiroz, Roy McDiarmid, Ron Heyer, George Zug, Jeremy Jacobs, and Steve Gotte (USNM), Jonathan Losos and José Rosado (MCZ), Fernando Castro-H (UV-C), Hussam Zaher (MZUSP), Laurie Vitt (OMNH), Tony Gamble (JFBM), Darell Frost and David Kizirian (AMNH), Jens Vindum, Robert Drewes, and Alan Leviton (CAS), Alan Resetar (FMNH), and Jim McGuire and Carol Spencer (MVZ). Virginia Abdala and Esteban Lavilla (Fundación Miguel Lillo) provided assistance with specimens, and Dan Scantlebury (University of Rochester) and Wolfgang Böhme and Philipp Wagner (Zoologisches Forschungsmuseum Alexander Koenig) kindly provided X-rays of *S. shrevei* and *S. dommeli*, respectively. This research was supported by the Gerald M. Lemole, M.D. Endowed Chair in Integrative Biology Fund, and by grant DEB 0844523 from the National Science Foundation of the United States.

APPENDIX 1

Specimens used in phylogenetic analyses (Sk = dry skeleton, C&S = cleared and stained, HRXCT = high-resolution X-ray computed tomography, XR = X-ray, * = ethanol-preserved specimens).

Aristelliger lar (AMNH R-50272 [Sk], USNM 259998–260007, 260009* [XR], USNM

260008 [C&S]), *Chatogekko amazonicus* (AMNH-R 138670 [C&S], AMNH R-138726 [C&S], AMNH R-132039 [C&S], AMNH R-132052 [C&S], MZUSP 91394*, OMNH 36262 [C&S], OMNH 37616 [C&S], OMNH 37274 [C&S], OMNH 37110 [C&S], OMNH 36712 [C&S], USNM 302283–302284*, USNM 124173*, USNM 200660–200663*, USNM 200664 [C&S], USNM 200665–200666*, USNM 288763*, USNM 288764 [C&S], USNM 288765–288788*, USNM 289031 [C&S], USNM 289061–289066*, USNM 290881–290882*, USNM 290904 [C&S], USNM 290944–290945*, USNM 303472–303473*, USNM 570538*, USNM 304122 304123*), *Coleodactylus brachystoma* (MZUSP no data [C&S], MZUSP 87385*), *Euleptes europaea* (USNM 014861* [XR], USNM 565911*[XR], USNM 58963 [C&S]), *Gonatodes albogularis* (AMNH R-71594[Sk], MVZ 83402 [C&S], UV-C No data [Sk]), *Gymnodactylus geckoides geckoides* (CAS 49397 [HRXCT]), *Hemidactylus brookii* (BMNH 1978.1472*), *Lepidoblepharis xanthostigma* (RT 1875 [C&S], USNM 313758*, USNM 313791 [C&S], USNM 313834*), *Narudasia festiva* (AMB 8717 [C&S], CAS 186290 [C&S]), *Phyllodactylus wirshingi* (CAS 175498 [C&S], RT 13860 [C&S]), *Pristurus carteri* (CAS 225349 [C&S], BMNH 1971.44 [Sk], JFBM 15821 [Sk]), *Pseudogekko smaragdinus* (USNM 197367 [C&S], USNM 198423 [C&S], USNM 198424 [C&S]), *Pseudogonatodes guianensis* (MZUSP 94826 [C&S], USNM 84970* [XR], USNM 166138* [XR], USNM 234574* [XR], USNM 316687* [XR], USNM 321059* [XR], USNM 333018* [XR], USNM 538260–538267* [XR], USNM 566327* [XR]); *Quedenfeldtia trachyblepharus* (FMNH 197682 [C&S], USNM 71113* [XR], USNM 196417* [XR], MVZ 178124) [C&S], *Saurodactylus mauritanicus* (BMNH 87.10.6.1.6 [Sk], FMNH 197462 [C&S], USNM 217454* [XR]), *Sphaerodactylus ciguapa* (MCZ R-186380 [Sk, XR]), *Sphaerodactylus roosevelti* (UPRRP 6376–6378 [C&S], UPRRP 6380–6381 [C&S], UPRRP 6488 [C&S], USNM 326986–326987* [XR], USNM 326996* [XR], USNM 327042* [XR]), *Sphaerodactylus klauberi* (UPRRP 6409–6421 [C&S], UPRRP 6423–6427 [C&S]), *Tarentola mauritanica* (AMNH R-71591 [Sk], AMNH R-144408 [C&S], BMNH 1913.7.3.36 [Sk], JFBM 15824 [Sk]), *Teratoscincus scincus* (BMNH 92.11.28.1 [Sk], CAS 101437 [C&S]), *Thecadactylus rapicauda* (AMNH R-59722 [Sk], AMNH R-75824 [Sk], AMNH R-85312 [Sk], BMNH 59.9.6.436 [Sk], USNM 220204 [Sk]).

APPENDIX 2

Specimens used for comparative purposes (Sk = dry skeleton, C&S = cleared and stained, HRXCT = high-resolution X-ray computed tomography, XR = X-ray, * = ethanol-preserved specimens).

Ailuronyx seychellensis (CAS 8421 [C&S]), *Aristelliger georgeensis* (CAS 176485 [HRXCT]), *Aristelliger praesignis* (AMNH R-146747 [C&S], AMNH R-71593 [Sk], AMNH R-71595 [Sk], BMNH 1964.1812 [Sk], BMNH 86.4.15.4 [Sk]), *Coleodactylus guimaraesi* (USNM 304122* [XR]), *Coleodactylus meridionalis* (MZUSP 88673*), *Coleodactylus septentrionalis* (MZSP 66554*, MZUSP 66556*, USNM 302285–302287* [XR], USNM 302337* [XR], USNM 302361* [XR], USNM 531620–531622* [XR], USNM 566300* [XR]), *Gonatodes annularis* (USNM 535787* [XR], USNM 535791* [XR]), *Gonatodes antillensis* (AMNH R-72642 [Sk], USNM 94980* [XR]), *Gonatodes ceciliae* (USNM 166159* [XR]), *Gonatodes humeralis* (RT 01198 [C&S], USNM 568645* [XR]), USNM 568647* [XR]), USNM 568658* [XR]), USNM 568663* [XR]), USNM 568677* [XR]), USNM 568681* [XR]), USNM 568682* [XR]), USNM 568684* [XR]), USNM 568692* [XR]), *Gonatodes taniae* (UPRRP 006045 [C&S]), *Lepidoblepharis buchwaldi* (USNM 234565* [XR], USNM 234569* [XR]), *Lepidoblepharis festae* (USNM 166140–166143* [XR]), *Lepido-*

blepharis heyerorum (USNM 217635* [XR]), *Lepidoblepharis peraccae* (UV-C 8999 [Sk]), *Pristurus crucifer* (USNM 72014* [XR], USNM 217452* [XR], USNM 217453* [XR]), *Pristurus insignis* (BMNH 1953.1.7.73 [Sk]), *Pseudogonatodes barbouri* (AMNH R-144395 [C&S], AMNH R-146746 [C&S], AMNH R-146752 [C&S], AMNH 146757 [C&S]), *Pseudogonatodes peruvianus* (USNM 343190* [XR], USNM 343191* [XR]), *Sphaerodactylus altavelensis* (USNM 328548* [XR]), *Sphaerodactylus argivus* (USNM 104597* [XR]), *Sphaerodactylus argus* (USNM 251977–251978* [XR]), *Sphaerodactylus ariasae* (USNM 541804–541805* [XR], USNM 541807–541810* [XR]), *Sphaerodactylus armstrongi* (RT 5255 [C&S], USNM 260053* [XR], USNM 260046* [XR], USNM 260051–260054* [XR]), *Sphaerodactylus asterulus* (USNM 328946* [XR], USNM 328949* [XR]), *Sphaerodactylus beattyi* (USNM 304480–304481* [XR]), *Sphaerodactylus cinereus* (AMNH R-49566 [C&S]; USNM 292296* [XR]), *Sphaerodactylus copei* (RT 10576 [C&S], USNM 118881* [XR]), *Sphaerodactylus corticola* (USNM 211428* [XR], USNM 220548–220552* [XR]), *Sphaerodactylus darlingtoni* (USNM 328962* [XR]), *Sphaerodactylus difficilis* (AMNH R-144413–144435 [C&S], USNM 328965* [XR]), *Sphaerodactylus elegans* (USNM 27625* [XR], USNM 27981* [XR]), *Sphaerodactylus gaigeae* (UPRRP 6428–6432 [C&S], UPRRP 6434–6436 [C&S]), *Sphaerodactylus goniorhynchus* (BMNH 1963.841*), *Sphaerodactylus gossei* (BMNH1964.1801-2 [Sk), *Sphaerodactylus ladae* (USNM 512248* [XR], USNM 512251* [XR], USNM 512253–512254* [XR]), *Sphaerodactylus leucaster* (USNM 197338* [XR]), *Sphaerodactylus levinsi* (RT 8283–8284 [Sk], USNM 220939* [XR], USNM 220921* [XR]), *Sphaerodactylus lineolatus* (BMNH 97.11.12.1*, UPRRP 3172 [C&S], USNM 120479* [XR], USNM 120497* [XR], USNM 12053* [XR], USNM 120504* [XR]), *Sphaerodactylus macrolepis* (UPRRP 6437–6445 [C&S], USNM 221462* [XR]), *Sphaerodactylus microlepis* (USNM 222901* [XR]), *Sphaerodactylus micropithecus* (USNM 229891* [XR]), *Sphaerodactylus millepunctatus* (AMNH R–16284* [XR]), *Sphaerodactylus monensis* (UPRRP 6454 [C&S]), *Sphaerodactylus nicholsi* (UPRRP 6383–6386 [C&S], UPRRP 63880 [C&S]), *Sphaerodactylus nigropunctatus* (AMNH R–73470 [Sk]; BMNH 1946.8.24.81*), *Sphaerodactylus notatus* (BMNH 1965.186*, USNM 494822* [XR]), *Sphaerodactylus oliveri* (USNM 140431* [XR], USNM 140435* [XR]), *Sphaerodactylus oxyrhinus* (USNM 292288–292289* [XR]), *Sphaerodactylus pacificus* (BMNH 1979.385–1979.386*, USNM 157531–157532* [XR]), *Sphaerodactylus parkeri* (USNM 328281* [XR]), *Sphaerodactylus parthenopion* (USNM 221593* [XR]), *Sphaerodactylus ramsdeni* (USNM 309772* [XR]), *Sphaerodactylus randi* (USNM 305427–305428* [XR]), *Sphaerodactylus rhabdotus* (USNM 292328* [XR]), *Sphaerodactylus richardsonii* (BMNH 1964.1801–2*, USNM 252126* [XR]), *Sphaerodactylus shrevei* (USNMFH 194578 [XR]), *Sphaerodactylus rosaurae* (BMNH 1946.8.16.60*, USNM 570196–570199* [XR], USNM 570204–570213* [XR]), *Sphaerodactylus ruibali* (USNM 78921* [XR]), *Sphaerodactylus sabanus* (USNM 27625* [XR], USNM 236098* [XR]), *Sphaerodactylus samanensis* (USNM 319135* [XR]), *Sphaerodactylus savagei* (USNM 260157* [XR]; *Sphaerodactylus scapularis*: BMNH 1901.3.29.6*, BMNH 1946.8.30.70*, BMNH 1902.729.1–2*, BMNH 1926.1.20*), *Sphaerodactylus semasiops* (BMNH 1968.326*, USNM 292294* [XR], USNM 305435* [XR]), *Sphaerodactylus sommeri* (USNM 292313* [XR]), *Sphaerodactylus sputator* (USNM 236118* [XR]), *Sphaerodactylus streptophorus* (USNM 541811* [XR], USNM 541813* [XR]), *Sphaerodactylus thompsoni* (USNM 328977* [XR]), *Sphaerodactylus townsendi* (UPRRP 6389–6400 [C&S], UPRRP 6402–6407 [C&S], USNM 291193* [XR]), *Sphaerodactylus vincenti* (USNM 286941* [XR], USNM 121648* [XR]), *Sphaerodactylus millepunctatus* (USNM 496644* [XR]), *Teratoscincus microlepis* (AMNH R-

88524 [Sk], BMNH 1934.10.9.14 [Sk]), *Teratoscincus przewalskii* (CAS 171013 [HRXCT], JFBM 15826 [Sk]), *Teratoscincus roborowskii* (JFBM 15828 [Sk]).

LITERATURE CITED

Al Hassawi, A. M. 2007. *A Comparative Anatomy of the Neck Region in Lizards*. Victoria, Trafford Publishing.

Alonso, J., A. Arillo, E. Barrón, J. C. Corral, J. Grimalt, J. F. López, R. López, X. Martínez-Delclòs, V. Ortuño, E. Peñalver, and P. R. Trincão. 2000. A new fossil resin with biological inclusions in Lower Cretaceous deposits from Alava (northern Spain, Basque-Cantabrian Basin). *Journal of Paleontology* 74: 158–178.

Angulo Guridi, F. J. 1866. *La Campana del Higo (Tradición Dominicana), La Ciguapa, Silvio*. Santo Domingo, Imprenta de García Hermanos.

Arnold, E. N. 2009. Relationships, evolution and biogeography of Semaphore geckos, *Pristurus* (Squamata, Sphaerodactylidae) based on morphology. *Zootaxa* 2060: 1–21.

Arnold, E. N., D. Azar, I. Ineich, and A. Nel. 2002. The oldest reptile in amber: a 120 million year old lizard from Lebanon. *Journal of Zoology* (*London*), 258: 7–10.

Arnold, E. N., and G. Poinar, Jr. 2008. A 100 million year old gecko with sophisticated adhesive toe pads, preserved in amber from Myanmar. *Zootaxa* 1847: 62–68.

Barbour, T. 1921. *Sphaerodactylus*. *Memoirs of the Museum of Comparative Zoology* 47: 217–278.

Bauer, A. M. 1990. Phylogeny and biogeography of the geckos of southern Africa and the islands of the western Indian Ocean: a preliminary analysis, pp. 274–284. *In* G. Peters and R. Hutterer eds. *Vertebrates in the Tropics*. Bonn, Zoologisches Forschungsinstitut und Museum A. Koenig.

Bauer, A. M., W. Böhme, and W. Weitschat. 2005. An Early Eocene gecko from Baltic amber and its implications for the evolution of gecko adhesion. *Journal of Zoology (London)* 265: 327–332.

Bauer, A. M., and W. R. Branch. 1995. The use of radiography in the anaysis of resin-embedded lizards. *Curator* 38: 185–189.

Bauer, A. M., and A. P. Russell. 1989. Supraorbital ossifications in geckos (Reptilia: Gekkonidae). *Canadian Journal of Zoology* 67: 678–684.

Böhme, W. 1984. Erstfund eines fossilien Kugelfingergeckos (Sauria: Gekkonidae: Sphaerodactylinae) aus Dominikanischem Bernstein (Oligozän von Hispaniola, Antillen). *Salamandra* 20: 212–220.

Böhme, W., and W. Weitschat. 1998. Redescription of the Eocene lacertid lizard *Nucras succinea* Boulenger, 1917 from Baltic amber and its allocation to *Succinilacerta* n. gen. *Mitteilungen des Geologisch-Paläontologischen Instituts der Universität Hamburg* 81: 203–222.

Böhme, W., and W. Weitschat. 2002. New finds of lizards in Baltic amber (Reptilia: Squamata: Sauria: Lacertidae). *Faunistische Abhandlungen Staatliches Museum für Tierkunde Dresden* 23: 117–130.

Borsuk-Białynicka, M., M. Lubka, and W. Böhme. 1999. A lizard from Baltic amber (Eocene) and the ancestry of the crown-group lacertids. *Acta Palaeontologica Polonica* 44: 349–382.

Bosch Gaviño, J. 1935. *Indios: Apuntes Históricos y Leyendas*. Santo Domingo, Editorial La Nación.

Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10: 295–304.

Conrad, J. L. 2008. Phylogeny and systematics of Squamata (Reptilia) based on morphology. *Bulletin of the American Museum of Natural History* 310: 1–182.

Conrad, J. L., and M. Norell. 2006. High-resolution X-ray computed tomography of an Early Cretaceous gekkonomorph (Squamata) from Öösh (Övorkhangai; Mongolia). *Historical Biology* 18: 405–431.

Daza, J. D. 2008. Cladistic analysis of the Gekkota (Reptilia) by means of craniological data. Ph.D. Dissertation. San Juan, University of Puerto Rico.

Daza, J. D., V. Abdala, R. Thomas, and A. M. Bauer. 2008. Skull anatomy of the miniaturized gecko *Sphaerodactylus roosevelti* (Squamata: Gekkota). *Journal of Morphology* 239: 1340–1364.

Daza, J. D., and A. M. Bauer. 2010. The circumorbital bones of the Gekkota (Reptilia: Squamata). *Anatomical Record* 293: 402–413.

de Queiroz, K., L.-R. Chu, and J. B. Losos. 1998. A second *Anolis* lizard in Dominican amber and the systematics and ecological morphology of Dominican amber anoles. *American Museum Novitates* 3249: 1–23.

Evans, S. E. 2008. The skull of lizards and tuatara, pp. 1–347. *In* C. Gans, A. S. Gaunt, and K. Adler eds. *Biology of the Reptilia*, Volume 20, *Morphology H* (*The Skull of Lepidosauria*). Ithaca, Society for the Study of Amphibians and Reptiles.

Frazzetta, T. H. 1962. A functional consideration of cranial kinesis in lizards. *Journal of Morphology* 111: 287–319.

Gamble, T., A. M. Bauer, G. R. Colli, E. Greenbaum, T. R. Jackman, L. J. Vitt, and A. M. Simons. 2011b. Coming to America: multiple origins of the

New World geckos. *Journal of Evolutionary Biology* 24: 231–244.

Gamble, T., A. M. Bauer, E. Greenbaum, and T. R. Jackman. 2008a. Evidence for Gondwanan vicariance in an ancient clade of gecko lizards. *Journal of Biogeography* 35: 88–104.

Gamble, T., A. M. Bauer, E. Greenbaum, and T. R. Jackman. 2008b. Out of the blue: a novel, trans-Atlantic clade of geckos (Gekkota, Squamata). *Zoologica Scripta* 37: 355–366.

Gamble, T., J. D. Daza, G. R. Colli, L. J. Vitt, and A. M. Bauer. 2011a. A new genus of miniaturized and pug-nosed gecko from South America (Sphaerodactylidae: Gekkota). *Zoological Journal of the Linnean Society* 163: 1244–1266.

Gauthier, J., R. Estes, and , and K de Queiroz. 1988. A phylogenetic analysis of Lepidosauromorpha, pp. 15–98. *In* R. Estes and G. Pregill eds. *Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L Camp.* Stanford, Stanford University Press.

Goloboff, P. A. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. *Cladistics* 15: 415–428.

Goloboff, P. A., and J. S. Farris. 2001. Methods for quick consensus estimation. *Cladistics* 17: S26–S34.

Goloboff, P. A., J. S. Farris, M. Källesjö, B. Oxelman, M. J. Ramírez, and C. A. Szumik. 2003b. Improvements to resampling measures of group support. *Cladistics* 19: 324–332.

Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2003a. T.N.T.: tree analysis using new technology. Version 1.0. http://www.zmuc.dk/public/phylogeny

Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24: 774–786.

Greer, A. E. 1976. On the ocurrence of stapedial foramen in living non-gekkonid lepidosaurs. *Copeia* 1976: 591–592.

Grimaldi, D. 1995. The age of Dominican amber, pp. 203–217. *In* K. B. Anderson and J. C. Crelling eds. *Amber, Resinite, and Fossil Resins.* Washington, American Chemical Society.

Grimaldi, D. 1996. *Amber. Window to the Past.* New York, American Museum of Natural History.

Grimaldi, D., and G. R. Case. 1995. A feather in amber from the Upper Cretaceous of New Jersey. *American Museum Novitates* 3126: 1–6.

Grimaldi, D., M. S. Engel, and P. C. Nascimbene. 2002. Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. *American Museum Novitates* 3361: 1–71.

Grismer, L. L. 1988. Phylogeny, taxonomy, classification, and biogeography of eublepharid geckos, pp. 369–469. *In* R. Estes and G. Pregill eds. *Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L Camp.* Stanford, Stanford University Press.

Harris, D. J. 1982. *The Sphaerodactylus* (Sauria: Gekkonidae) of South America. *Occasional Papers of the Museum of Zoology, University of Michigan* 59: 1–42.

Hass, C. A. 1991. Evolution and biogeography of West Indian *Spaherodactylus* (Sauria: Gekkonidae): a molecular approach. *Journal of Zoology (London)* 225: 525–561.

Hass, C. A. 1996. Relationships among the West Indian geckos of the genus *Sphaerodactylus*: a preliminary analysis of mitochondrial 16s ribosomal RNA sequences, pp. 175–194. *In* R. Powell and R. W. Henderson eds. *Contributions to West Indian Herpetology: A Tribute to Albert Schwartz.* Ithaca, Society for the Study of Amphibians and Reptiles.

Hedges, S. B. 2011. *Caribherp: West Indian Amphibians and Reptiles*, Beta Version. University Park, Pennsylvania State University, http://www.caribherp.org

Hedges, S. B., and R. Thomas. 2001. At the lower size limit in amniote vertebrates: a new diminutive lizard from the West Indies. *Caribbean Journal of Science* 37: 168–173.

Henderson, R. W., and R. Powell. 2009. *Natural History of West Indian Reptiles and Amphibians.* Gainesville, University Press of Florida.

Hoffstetter, R., and J.-P. Gasc. 1969. Vertebrae and ribs of modern reptiles, pp. 201–210. *In* C. Gans ed. *Biology of the Reptilia*, Volume 1, *Morphology A.* New York, Academic Press.

Iturralde-Vinent, M. A. 2001. Geology of the amber-bearing deposits of the Greater Antilles. *Caribbean Journal of Science* 37: 141–167.

Itturralde-Vinent, M. A., and R. D. E. MacPhee. 1996. Age and paleogeographical origin of Dominican amber. *Science* 273: 1850–1852.

Jollie, M. T. 1960. The head skeleton of the lizard. *Acta Zoologica (Stockholm)* 41: 1–54.

Katinas, V. 1983. *Baltijos Gintaras.* Vilnius, Mokslas.

Kluge, A. G. 1962. Comparative osteology of the eublepharid genus *Coleonyx* Gray. *Journal of Morphology* 110: 299–332.

Kluge, A. G. 1967. Higher taxonomic categories of gekkonid lizards and their evolution. *Bulletin of the American Museum of Natural History* 135: 1–60.

Kluge, A. G. 1983. Cladistic relationships among gekkonid lizards. *Copeia* 1983: 465–475.

Kluge, A. G. 1995. Cladistic relationships of Sphaerodactyl lizards. *American Museum Novitates* 3139: 1–23.

KLUGE, A. G. 2001. Gekkotan lizard taxonomy. *Hamadryad* 26: 1–209.

KOSMOWSKA-CERANOWICZ, B., R. KULICKA, AND G. GIERLOWSKA. 1997a. A lizard found in Baltic amber. Gdańsk Museum of the Earth, Scientific Conferences, Abstracts 9: 23–24.

KOSMOWSKA-CERANOWICZ, B., R. KULICKA, AND G. GIERLOWSKA. 1997b. Nowe znalezisko jaszczurki w bursztynie baltyckim. *Przegląd Geologiczny* 45: 1028–1030.

KRUMBIEGEL, G. 1998. Eidechsenfund im Baltischen Bernstein. *Fossilien* 1998: 231–235.

LARSSON, S. G. 1978. *Baltic Amber—A Palaeobiological Study*. Entomograph Volume 1. Klampenborg, Scandinavian Science Press Ltd,

LAZELL, J. D., JR. 1965. An *Anolis* (Sauria, Iguanidae) in amber. *Journal of Paleontology* 39: 379–382.

LOSOS, J. B. 2009. *Lizards in an Evolutionary Tree. Ecology and Adaptive Radiation of Anoles*. Berkeley, University of California Press.

LOSOS, J. B., T. R. JACKMAN, A. LARSON, K. DE QUEIROZ, AND L. RODRIGUEZ-SCHETTINO. 1998. Contingency and determinism in replicated adaptive radiations of island lizards. *Science* 279: 2115–2118.

MACPHEE, R. D. E., AND D. A. GRIMALDI. 1996. Mammal bones in Dominican amber. *Nature* 380: 489–490.

MACPHEE, R. D. E., M. A. ITURRALDE-VINENT, AND E. S. GAFFNEY. 2003. Domo de Zaza, an Early Miocene vertebrate locality in south-central Cuba, with notes on the tectonic evolution of Puerto Rico and the Mona Passage. *American Museum Novitates* 3394: 1–42.

MCDOWELL, S. B. 2008. The skull of serpentes, pp. 467–620. *In* C. Gans, A. S. Gaunt, and K. Adler eds. *Biology of the Reptilia*, Volume 21, *Morphology I (The Skull and Appendicular Locomotor Apparatus of Lepidosauria)*. Ithaca, Society for the Study of Amphibians and Reptiles.

MONTERO, R., AND C. GANS. 2008. An atlas of amphisbaenian skull anatomy, pp. 621–738. *In* C. Gans, A. S. Gaunt, and K. Adler eds. *Biology of the Reptilia*, Volume 21, *Morphology I (The Skull and Appendicular Locomotor Apparatus of Lepidosauria)*. Ithaca, Society for the Study of Amphibians and Reptiles.

NOBLE, G. K. 1921. The bony structure and phyletic relations of *Sphaerodactylus* and allied lacertilian genera, with the description of a new genus. *American Museum Novitates* 4: 1–16.

OELRICH, T. M. 1956. The anatomy of the head of *Ctenosaura pectinata* (Iguanidae). *University of Michigan Museum of Zoology, Miscellaneous Publications* 94: 1–122.

PARKER, H. W. 1926. The Neotropical lizards of the genera *Lepidoblepharis*, *Pseudogonatodes*, *Lathrogecko*, and *Sphaerodactylus*, with the description of a new genus. *Annals and Magazine of Natural History* Series 9 17: 291–301.

PAYNE, S. L., C. M. HOLLIDAY, AND M. K. VICKARYOUS. 2011. An osteological and histological investigation of cranial joints in geckos. *The Anatomical Record* 294: 399–405.

PÉREZ, J. B. 1972. *Geografía y Sociedad.* Santo Domingo, Editora del Caribe.

PERRICHOT, V., L. MARION, D. NÉRAUDEAU, R. VULLO, AND P. TAFFOREAU. 2008. The early evolution of feathers: fossil evidence from Cretaceous amber of France. *Proceedings of the Royal Society Biological Sciences* Series B 275: 1197–1202.

PERRICHOT, V., AND D. NÉRAUDEAU. 2005. Reptile skin remains in the Cretaceous amber of France. *Comptes Rendus Palevol* 4: 47–51.

POINAR, G. O. JR. 1992. *Life in Amber*. Stanford, Stanford University Press.

POINAR, G. O., JR., AND D. C. CANNATELLA. 1987. An Upper Eocene frog from the Dominican Republic and its implication for Caribbean biogeography. *Science* 237: 1215–1216.

POINAR, G. O. JR., AND R. POINAR. 1994. *The Quest for Life in Amber*. Reading, Helix Books.

POINAR, G. O. JR., AND R. POINAR. 1999. *The Amber Forest, a Reconstruction of a Vanished World.* Princeton, Princeton University Press.

POLCYN, M. J., J. V. ROGERS II, Y. KOBAYASHI, AND L. L. JACOBS. 2002. Computed tomography of an *Anolis* lizard in Dominican amber: systematic, taphonomic, biogeographic, and evolutionary implications. *Palaeontologia Electronica* **5:** 13.

RIEPPEL, O. 1980. Green anole in Dominican amber. *Nature* 286: 486–487.

RIEPPEL, O. 1984. The structure of the skull and jaw adductor musculature of the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zoological Journal of the Linnean Society* 82: 291–318.

RIEPPEL, O. 1985. The recessus scalae tympani and its bearing on the classification of reptiles. *Journal of Herpetology* 19: 373–384.

RITZKOWSKI, S. 1997. K-Ar-Altersbestimmung der Bernsteinführenden Sedimente des Samlandes (Paläogen, Bezirk Kaliningrad). *Metalla* (Sonderheft) 66: 19–23.

RIVERO-BLANCO, C. V. 1976. *Osteology of the Lizard* Gonatodes humeralis (*Guichenot*) *and Other Representative Species of the Genus*. M.S. Thesis. College Station, Texas A & M University.

Rivero-Blanco, C. V. 1979. The neotropical lizard genus *Gonatodes* Fitzinger (Sauria: Sphaerodactylinae). Ph.D. Dissertation. College Station, Texas A & M University.

Russell, A. P., and A. M. Bauer. 2008. The appendicular locomotor apparatus of *Sphenodon* and normal-limbed squamates, pp. 1–466. *In* C. Gans, A. S. Gaunt, and K. Adler eds. *Biology of the Reptilia*, Volume 21, *Morphology I (The Skull and Appendicular Locomotor Apparatus of Lepidosauria)*. Ithaca, Society for the Study of Amphibians and Reptiles.

Russell, D. A. 1967. Systematics and morphology of American mosasaurs. *Bulletin of the Peabody Museum of Natural History* 23: [i]–vii, 1–241.

Schwartz, A., and O. Garrido. 1985. The Cuban lizards of the genus *Sphaerodactylus* (Sauria, Gekkonidae). *Milwaukee Public Museum Contributions in Biology and Geology* 62: 1–67.

Schwartz, A., and E. D. Graham, Jr. 1980. The *shrevei* group of Hispaniolan *Sphaerodactylus* (Reptilia, Gekkonidae). *Tulane Studies in Zoology and Botany* 22: 1–15.

Schwartz, A., and R. W. Henderson. 1991. *Amphibians and Reptiles of the West Indies. Descriptions, Distributions and Natural History*. Gainesville, University Press of Florida.

Schwartz, A., and R. Thomas. 1983. The *difficilis* complex of *Sphaerodactylus* (Sauria, Gekkonidae) of Hispaniola. *Bulletin of Carnegie Museum of Natural History* 22: 1–60.

Sontag, E. 2008. Kolekcja Muzeum Inkluzji w Bursztynie Uniwersytetu Gdańskiego po 10 latach działalności/ The collection of the Museum of Amber Inclusions at the University of Gdańsk: looking back at 10 years of existence. *Bursztynisko* 31: 27–34.

Thomas, R. 1975. The *argus* group of West Indian *Sphaerodactylus* (Sauria: Gekkonidae). *Herpetologica* 31: 177–195.

Thomas, R. 1999. The Puerto Rico area, pp. 169–179. *In* B. I. Crother ed. *Caribbean Amphibians and Reptiles*. London, Academic Press.

Thomas, R., S. B. Hedges, and O. H. Garrido. 1992. Two new species of *Sphaerodactylus* from eastern Cuba (Squamata: Gekkonidae). *Herpetologica* 48: 358–367.

Thomas, R., and A. Schwartz. 1966. *Sphaerodactylus* (Gekkonidae) in the Greater Puerto Rico region. *Bulletin of the Florida State Museum* 10: 193–260.

Thomas, R., and A. Schwartz. 1983. Variation in Hispaniolan *Sphaerodactylus* (Sauria: Gekkonidae), pp. 86–98. *In* A. G. J. Rhodin and K. Miyata eds. *Advances in Herpetology and Evolutionary Biology. Essays in Honor of Ernest E Williams*. Cambridge, Museum of Comparative Zoology, Harvard University.

Ubiñas Renville, J. G. 2000. *Mitos, Creencias y Leyendas Dominicanas*. Santo Domingo, Ediciones Librería La Trinitaria.

Ubiñas Renville, J. G. 2003. *Historias y Leyendas Afro-Dominicanas*. Santo Domingo, Editora Manatí.

Uetz, P. 2011. *The Reptile Database*. http://www.reptile-database.org/

Webb, M. 1951. The cranial anatomy of the South African geckoes *Palmatogecko rangei* (Andersson) and *Oedura karroica* (Hewitt). *Annals of the University of Stellenbosch* 27A: 131–165.

Weitschat, W., and W. Wichard. 2002. *Atlas of Plants and Animals in Baltic Amber*. München, Verlag Dr. Friedrich Pfeil.

Werner, Y. L. 1971. The ontogenetic development of the vertebrae in some gekkonid lizards. *Journal of Morphology* 133: 41–92.

Williams, D. M. 1976. West Indian anoles: a taxonomic and evolutionary summary. 1. Introduction and a species list. *Breviora* 440: 11–21.